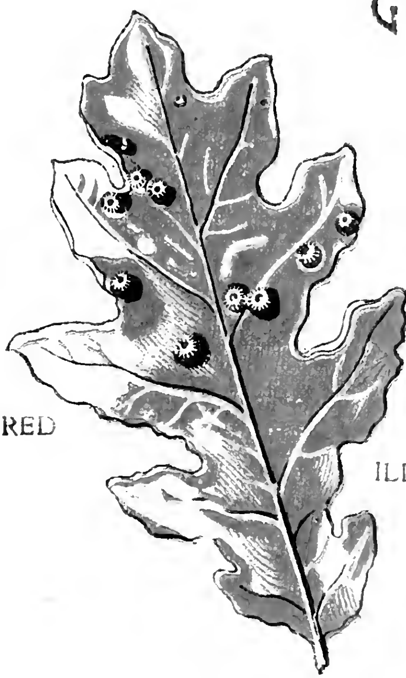
Alternating Generations
a Study of
Oak Galls
and
Gall Flies



WITH COLOURED ILLUSTRATIONS OF 42 SPECIES

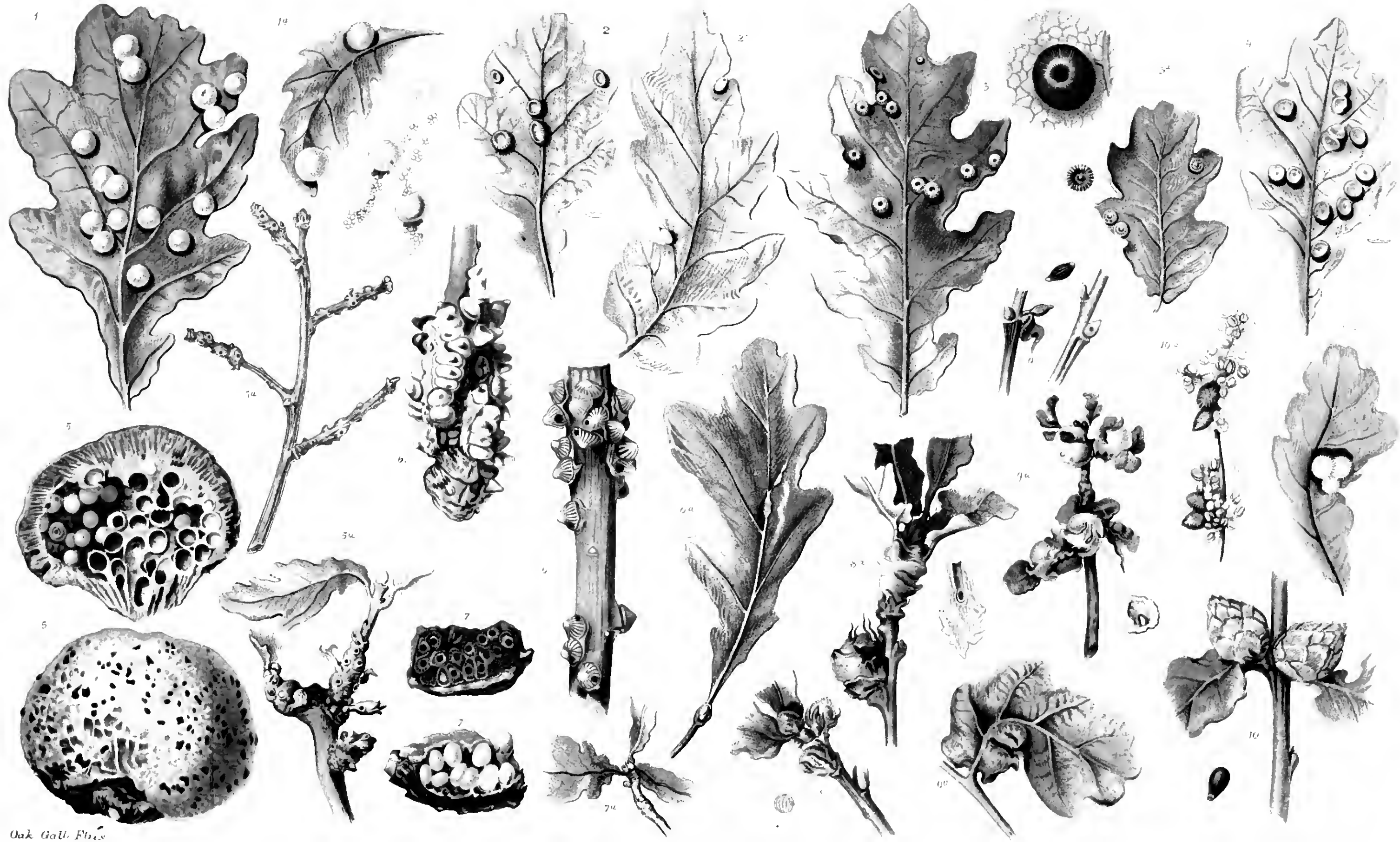
Adler & Straton

ALTERNATING GENERATIONS

ADLER & STRATON

London
HENRY FROWDE
Oxford University Press Warehouse
Amen Corner, E.C.

New York
MACMILLAN & CO., 66 FIFTH AVENUE



Oak Gall Flies

University Press Oxford.

Alternating Generations

A Biological Study of Oak Galls and Gall Flies

By Hermann Adler, M.D.

Schleswig

TRANSLATED AND EDITED BY

CHARLES R. STRATON

F.R.C.S. ED., F.E.S.

WITH ILLUSTRATIONS

Oxford

AT THE CLARENDON PRESS

1894

Oxford

PRINTED AT THE CLARENDON PRESS

BY HORACE HART, PRINTER TO THE UNIVERSITY

EDITOR'S PREFACE

WHILE pursuing the study of galls as a branch of comparative pathology, I was fortunate enough to become acquainted with Dr. Adler's monograph of Alternating generations in oak gall-flies.

The originality of the matter, and the important light which it threw on some of the great biological problems of the day, induced me to ask his permission to publish it in an English dress. I have to thank him for the generous manner in which he placed his work, and the beautiful drawings which accompanied it, at my disposal. Unfortunately the stones from which the illustrations were printed had been broken up, but I venture to think that they have been very faithfully reproduced.

In the Introduction, and especially in the description of *Cynips Kollari* in the Appendix, I have used freely the writings of Dr. Beyerinck and Professor Mayr. I have added an analytical table of galls, a short bibliography, and a list of the Cynipidae. I have enclosed my own notes to the text in brackets, and in these I have given the synonyms of each species, its popular name, the inquilines and parasites which

have been reared from it, and the species of oak on which it is recorded as having been found.

My grateful acknowledgements are due to Dr. Adler, Mr. E. A. Fitch, and Mr. A. Ehrmann for their assistance in correcting the proofs, and to Professor Mayr and Baron C. R. Osten-Sacken for information on special points.

C. R. S.

West Lodge,
Wilton,
Salisbury.

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INTRODUCTION

A GALL is an abnormal growth of plant tissue produced by animal agency acting from within. All the natural orders of plants include species which are liable to be made use of by insects in this way. Each is visited by its own special gall-maker, which need not necessarily belong to the Cynipidae, for gall-makers are also found among the Coleoptera, Lepidoptera, Diptera, Nematoda [1], and in other classes. Any organ of the plant may become the seat of this hyperplasia, but the form which the gall ultimately assumes is governed by the potentialities of growth in the part attacked, and by the nature of the animal excitation present. The rose and some Compositae produce well known galls, but the oak is the favourite home of the Cynipidae. In this monograph Dr. Adler has described those oak-galls and gall-flies most commonly found in this country, with the exception of *Cynips Kollari*, the Devonshire marble-gall, which does not occur in Germany north of the Elbe; as it is however one of the most familiar galls on English oaks, a description of it has been added in the appendix. Before Dr. Adler

[1] H. Charlton Bastian, 'Monograph of the Anguillulidae,' *Lin. Soc. Trans.* vol. xxv, 1866.

had demonstrated the existence of cyclical propagation, many curious explanations were offered, in order to account for the lengthened interval that elapses between the death of one generation and the appearance of the next. The currant-gall, for example, appears on the male catkins of the oak in May, the fly quits the gall in June, lives for a few days only, and nothing more is seen until the male catkin appears again next May. What had become of the eggs in this long interval? Spontaneous generation of the insect, within a gall that had no external opening, had its advocates. Later it was believed that a form of metempsychosis took place, and galls were among the stepping-stones in the path of organic evolution, by which the vegetable passed into the animal soul. By some it was supposed that the eggs, found in the fly in June, reached the ground, whence they were drawn up, mingled with the sap, and arrested next spring in the leaves or flowering catkins, there to form the currant-galls again. Dr. Adler, by proving the existence of cyclical propagation, has shown that the interval between the appearance of the currant gall-fly in one spring, and its reappearance in the next, is occupied by another agamous generation. But while he showed that this rule holds good for the majority of species, he has also demonstrated that, in some at least, no sexual generation now exists.

Pliny[1] knew that a fly was often produced in a gall, but he did not associate it with the cause of gall-growth; on the contrary, he thought galls grew in a night, like fungi. Many early observers, however, considered them as insect productions and were aware that a variety of insects emerged from them; but the attention which some of these authors bestowed upon this subject was

[1] Pliny, *Nat. Hist.* xvi. 9, 10; xxiv. 5.

not always due to its biological interest. Mathiolus, one of the best of the commentators of Dioscorides, and a believer in spontaneous generation, declared that weighty prognostications as to the events of the year could generally be deduced by observing whether galls contained spiders, worms, or flies. Most of the older writers describe gall-flies, which are now known to be agamous, as possessing males; but their descriptions are often perfectly clear, and the flies can be recognized as the males of one of the Torymidae, or of some other species of parasite. There is no reason to think that any males of agamous species were actually in existence at the time when these authors wrote.

The earliest systematic writer on galls was Marcellus Malpighi, Physician to Innocent XII. He was Professor of Medicine at Bologna, and afterwards at Messina, and his treatise[1] 'De gallis,' published in 1686, gives an extremely accurate description of the galls then found in Italy and Sicily. Dr. Derham, Canon of Windsor, in the notes to his Boyle Lectures (1711–1712) compares Malpighi's account with the galls then found in England, and says, 'I find Italy and Sicily more luxuriant in such productions than England, at least than the parts about Upminster (where I live) are. For many, if not most, of the galls about us are taken notice of by him, and several others besides that I have never met with, although I have for many years as critically observed all the excrescences and other morbid tumours of vegetables as is almost possible, and do believe that few of them have escaped me[2].'

Malpighi's work does not appear to have been known either to Linnaeus or Fabricius; they include

[1] *Dioscorides*, i. 146, Paris, 1549.

[2] W. Derham, F.R.S., *Physico-theology*, iii. c. 6.

inquilines and parasites under the genus Cynips, indeed St. Hilaire, Latreille, and Olivier reserve the name Cynips for certain Chalcididae, and use Diplolepis for the true gall-maker, but with few exceptions subsequent writers have applied the general name Cynips to the gall-makers. It is well, however, to bear this change of nomenclature in mind, when the males of certain species are said to have been found [1]. Réaumur has left excellent descriptions and drawings of many species of galls [2], but the first to bring order out of the confusion in which the *Cynipidae* still remained, was Theodor von Hartig of Brunswick [3]. He greatly improved the existing classification of this family and carefully pointed out the true relationship which the various dwellers in galls bore to each other. He arranged gall inhabitants into three classes; first, the gall-makers which he compared to the actual householders; secondly, inquilines, guest-flies, cuckoo-flies or lodgers, who take up their quarters uninvited within the gall, and live on its food stores, but do not directly aim at the gall-maker's life; and thirdly, parasites who deposit their eggs on the larvae of their host or his lodgers, with the object of destroying them, and who are therefore murderers. Besides those living in a state of symbiosis, there are also true commensals in some galls.

It is the simultaneous presence of these various classes that frequently gives rise to confusion in carrying out breeding experiments. *Synergi* among inquilines resemble true gall-making species so closely, that caution

[1] Westwood, *Zoological Journal*, No. 13; Cameron, P., *British Phyt. Hymen.* vol. iii. p. 140.

[2] Réaumur, *Mémoires pour servir à l'histoire des insectes*, 1734–42.

[3] Hartig, 'Ueber die Familien der Gallwespen,' *Germar's Zeitschr. f. d. Ent.* II. Heft i. p. 176, 1840; III. 322-358, 1841; IV. 395, 1843.

is always necessary to see that the gall-maker, and not a Synergus, has been obtained [1]. Both Malpighi and Canon Derham were aware of the attacks of parasites, and actually saw galls pierced by them. The latter says, 'I apprehend we see many vermicules, towards the outside of many oak-apples, which I guess were not what the primitive insects laid up in the gem from which the oak-apple had its rise, but from some supervenient additional insects, laid in after the apple was grown, and whilst it was tender and soft [2].' Ratzeburg, a forester like Hartig, in his beautiful 'Forstinsekten' [3] corroborated Hartig's division of gall-dwellers. Giraud, Schenck, Reinhard, Taschenberg, Schlechtendal, Wachtl, Förster, and Lichtenstein, have since each advanced our knowledge of the Cynipidae, and the history of galls generally has been admirably written by Lacaze-Duthiers. The entomologists of America have not been behind those of Europe; Baron C. R. Osten-Sacken, before he quitted America in 1877, had discovered eighteen new species; Bassett, thirty species, and Walsh and Riley had each added much to our knowledge. Professor Gustav Mayr of Vienna has not only increased largely the work of previous observers, but has arranged all that is known of gall-makers and gall-dwellers in a series of admirable monographs [4] and has

[1] See Walker, *Ent. Mag.* vii. p. 54.

[2] Derham, *Physico-theology*, iii. p. 389.

[3] Ratzeburg, *Die Forstinsekten*, vol. iii, Berlin, 1844.

[4] Mayr, G., *Die mitteleuropäischen Eichengallen in Wort und Bildern*, Wien, 1870-71; *Die Einmiethler der mitteleuropäischen Eichengallen*, Wien, 1872; *Die europäischen Cynipiden-Gallen mit Ausschluss der auf Eichen vorkommenden Arten*, Wien, 1876; *Die europäischen Torymiden*, Wien, 1874; *Encyrtiden*, 1876; *Olinx*, 1877; *Eurytoma*, 1878; *Telenomus*, 1879; *Die Genera der gallenbewohnenden Cynipiden*, Wien, 1881; *Die europäischen Arten der gallenbewohnenden Cynipiden*, Wien, 1882.

drawn up excellent analytical tables of species. In this country Westwood, Halliday, Walker, and Fitch have all done good work, and Mr. Peter Cameron [1], in his account of the Phytophagous Hymenoptera, just completed for the Ray Society, has brought together an immense amount of valuable material, new and old.

Dr. Adler began his observations on gall-flies in 1875, and added certain new species described in these pages. His important work, however, was the unfolding of their life-history; proving that while many species were linked together in alternate agamous and sexual generations, others remained wholly agamous.

Among biologists theories of dimorphism and metagenesis had been discussed in connexion with the Cynipidae and were current as early as 1865 [2]; in 1873 Bassett announced his theory of seasonal dimorphism [3]; and in the same year Riley established the existence of alternation of generations between *Cynips operator* and *Cynips operatola* [4]. The numerous publications of Thomas and Frank have cleared up many special points, and Beyerinck [5] in an admirably illustrated monograph, full of original work and careful reasoning, has added much both from a botanical and zoological point of view.

The existence of alternating generations in living

[1] Peter Cameron, *A Monograph of the British Phytophagous Hymenoptera*, 4 vols. 1882–1893. Ray Society.

[2] Reinhard, 'Die Hypothesen über die Fortpflanzungsweise bie den eingeschlechtigen Gallwespen,' *Berlin. Ent. Zeitschr.* vol. ix. 1865.

[3] Bassett, *Canadian Entomol.* vol. v, pp. 91–94, May, 1873.

[4] Riley, *American Naturalist*, vol. vii. p. 519, 1873.

[5] Beyerinck, Dr. M. W., 'Beobachtungen über die ersten Entwicklungsphasen einiger Cynipidengallen,' *Natuurk. Verh. der Koninkl. Akademie*, Deel xxii.

organisms was first discovered by Chamisso[1], the author of 'Peter Schlemihl,' who in 1815 accompanied the Chancellor Rumjanzow's expedition as naturalist in a voyage round the world. He noticed that among the Salpae a solitary salpa gave rise to a generation of a different form, united in chains of twenty or more, and that each link of this 'associated' form again produced the 'solitary' form. He concluded that all solitary salpae produced chains, and on the other hand that all those in associated chains were the parents of solitary ones; so that a salpa mother was not like its daughter or its own mother, but resembled its granddaughter and its grandmother. At first the accuracy of Chamisso's observations was doubted, chiefly for the reason that no similar phenomenon was then known in nature. By degrees, however, facts began to accumulate; in hydroids and flukes similar generation-cycles were observed, and in 1842 Steenstrup[2] collected all that was known on the subject of alternating generations into a monograph published in Danish and subsequently translated into German and English. He described this mode of reproduction as 'a peculiar form of fostering the young in the lower classes of animals.'

In 1849 the late Professor Owen[3] suggested the existence of a residual germ-force in the cells of the apparently asexual generation, and thought that alternating generations were due 'to the retention of certain of the progeny of the primary impregnated germ-cell, or in other words to the germ-mass, with so much of the spermatic force inherited by the retained germ-cells from

[1] Adalbert de Chamisso, *De Animalibus*, Fasc. i, De Salpa, Berlin, 1819.

[2] J. J. S. Steenstrup, *Ueber den Generationswechsel*, Kopenhagen, 1842, and Ray Society, 1845.

[3] R. Owen, *Parthenogenesis*, 1849.

the parent cell or germ-vesicle, as suffices to set on foot and maintain the same series of formative actions as those which constituted the individual containing them': and this may be taken as the earliest suggestion of the continuity of the germ-plasm.

Fresh instances of this class of phenomena have steadily accumulated, in which the life-cycle of the species may be represented by two or more generations, differing in form and organization, existing under different conditions, and reproducing themselves in different ways.

The simplest cyclical rhythm occurs in reproduction by metagenesis, where a sexual and asexual form alternate; this is the law of development in Medusae and Trematoda. In heterogenesis a sexual and an agamous generation alternate, and in this rhythm the agamous may be juvenile or adult; in Cecidomyia, for example, the parthenogenetic generation reproduces itself when still immature, while in the Cynipidae, on the other hand, it does so only when perfectly developed. Another variety occurring between one hermaphrodite and one sexual form, is seen in *Angiostomum nigrovenosum*, the lung parasite of the frog; and a still more perfect alternation is found in the thread worm of the snail, *Leptoptera appendiculata*, where two perfectly formed sexual generations are linked in a cycle.

Sometimes the sexual or asexual member of the cycle may be complex. The liver-fluke of the sheep gives rise to an active ciliated aquatic embryo, which, after a time, pierces and enters a water-snail to become a passive sporocyst; from its germ-cells *rediae* are formed within the sporocyst, and after several asexual generations, they give rise to minute *cercariae*, which leave the snail and creep up the stalks of grass; here they

become encysted, are eaten, and grow within the sheep to become adult sexual flukes. In this series the *Cercaria* and fluke form members of the sexual division; all the others are members of the asexual division of the cycle.

In all cyclical propagation, whether in the animal or vegetable kingdom, there is a tendency for one generation to become subordinated to the other. In flowering plants the sexual is subordinated to the asexual, and even some ferns exhibit a similar tendency, a fern-plant rising vegetatively from the prothallus; while in other ferns there is a tendency to apospory, a fern-prothallus springs from the site of the spores, and the asexual becomes subordinated to the sexual. In flukes, in the same way, *rediae* may be budded off from the sporocyst and the species be continued without ever actually becoming sexual. In the Cynipidae it will be seen that in some, like *Cynips Kollari*, the sexual generation has been wholly subordinated to the asexual, and in others, like *Rhodites rosae*, this process is still going on and males are becoming functionless and extinct.

Leuckart[1] regarded interpolated generations as larval states, and following his teaching, Lichtenstein[2] looked upon the agamous as larval stages of the sexual species. He believed that the biological evolution of a gall-fly extended from the time when a female emerged from a true egg in a condition to be fecundated by the male, until another egg was reached presenting the same conditions. All other stages he considered as larval, although in them reproduction by budding was possible, and he held that in this way insects might go on reproducing themselves indefinitely without ever reaching

[1] R. Leuckart, *Zur Kenntniss d. Generationswechsels u. d. Parthenog. b. d. Insekten*, 1858.

[2] J. Lichtenstein, *Les Cynipides*, 1881, p. x.

the perfect state. Certain Phylloxeridae reproduce themselves by subterranean budding, without ever arriving at the winged and sexual forms: he regarded this as analogous to the multiplication of plants by suckers, without the intervention of seed. He compared the life-history of gall-flies with that of Phylloxera, and gave it as his opinion that, among the gall-flies, the individuals of *Neuroterus lenticularis* had been mistaken for females, because they possessed an ovipositor and eggs, that, properly speaking, they had no sex, but were only larval forms of *Spathegaster baccarum*, their so-called eggs being gemmations.

It is difficult to regard species which have a perfect female form, and ovaries filled with perfect eggs, as being perpetually in the larval state, because they are wholly agamous and have no males. In *Rhodites rosae*, as has been said, the few males found are functionless, and are disappearing; it seems therefore more in accordance with facts to speak of the individuals of agamous species as females, the males of which have ceased to appear. Although the Aphides are scarcely comparable to the Cynipidae, since they possess a form which is asexual, they may nevertheless be arranged, like the Cynipidae, in alternate generations, without having recourse to the larval theory.

The importance of sexual reproduction has been greatly exaggerated, and there seems no good ground for assuming that a generation ought to extend from one fecundated egg to another. In *Cynips Kollari*, and many others, no sexual generation is known; the flies all possess perfect female forms, but they are agamous and have the power of reproducing themselves by parthenogenetic eggs. At the same time it is difficult to believe that the agamous can be the primitive

form; or that perfectly formed sexual organs could have been evolved unless the sexual had been the earlier generation.

The power of producing parthenogenetic eggs is widely distributed among the arthropods, and appears to come into operation whenever it secures the existence of the species more effectually than sexual reproduction. When at one season of the year sexual, and at another agamous, reproduction is the more beneficial, then heterogeny will be found to prevail. In one group amphimixis has been wholly abandoned, but its members are enormously prolific, and their eggs have the power of resting over more than one year. By means of partial parthenogenesis, a much more rapid increase is ensured than could have been possible, in the same time, by sexual reproduction only. Every individual of the winter generation, unhindered by the requirements of fertilization, is engaged in laying eggs; the number of the sexual individuals hatched from these eggs is consequently enormously greater than it could have been, had only half the winter generation been of the female sex, and had that half, in order to be fruitful, been dependent on the chances of fecundation. When generations alternate, there are alternating advantages to the species. The winter generations emerge from the gall at a time when pairing is not easy, and it is a distinct gain to the race when every individual has the power of reproducing itself independently. The summer generations, on the contrary, appear in halcyon days, when there is nothing to mar their nuptial flight, and then the species obtains greater variation, and those physiological advantages of amphimixis which parthenogenesis cannot afford.

But amphimixis is in no way essential to heredity.

The oak gall-flies about to be described will be found to afford examples of heredity occurring among purely agamous species, as well as among those which alternate between an agamous and a sexual generation. The characters of each generation are inherited and passed on in two perfectly distinct streams. The advance which has in recent times been made towards a clearer comprehension of heredity, is in great measure due to the influence of Weismann[1], who, by discarding the idea that sexual reproduction is in any way fundamental or essential to life, has led us to regard the facts of heredity wholly untrammelled by it. Amphimixis undoubtedly has its advantages, but descent may be continuous in the female line, or there may even be a male parthenogenesis[2].

To understand the mechanism by which alternation of generations is brought about, it is necessary to recall the minute structure of the sexual cells, and especially the behaviour of their nuclear contents; and to observe the difference in the extrusion of the polar cells, as occurring in the eggs of parthenogenetic and sexual species.

The changes in the ovum during nuclear division are briefly these[3]. After a resting stage the chromatin granules, which there is reason to believe are the material bearers of hereditary qualities, appear as a thread, apparently, spirally coiled within the nucleus. An accessory nucleus forms and divides into two; at each pole of its achromatic spindle is placed a centrosome with its surrounding attraction-sphere; the nuclear membrane disappears; the chromatin

[1] Weismann, *Essays on Heredity*, vol. ii. p. 86, 1893.

[2] Ibid. vol. i. p. 253; Schenck, *Handbuch der Botanik*, Bd. ii. p. 219.

[3] Weismann, *Essays on Heredity*, vol. ii. p. 118.

granules become aggregated into rod-like chromosomes of equal length and of constant number in each species; these are formed at the equator of the spindle, and split by longitudinal fission, so that their number becomes doubled. One star of chromosomes is drawn to the centrosome at each pole of the spindle, and thus two daughter-nuclei, which for convenience I will term oocytes, are formed, of unequal size; the smaller one being extruded as the first polar body. In the parthenogenetic egg this completes the division, but in the sexual egg a second nuclear division follows immediately on the first without a resting stage; the oocyte divides into two oozoa, and one oozoon, containing half the chromosomes, is extruded as the second polar body. The oocyte which forms the first polar body is observed to split into two oozoa after extrusion.

In this way three of the oozoa which have arisen from the division of the primitive germ-cell have become polar bodies, while the remaining oozoon, containing one half the number of chromosomes which the primitive germ-cell contained, is left in the nucleus, functional or capable of development.

Within the spermatic tubes of the male, corresponding changes take place in the primitive sperm-cell. Its chromosomes are doubled and it divides into two spermatocytes (spermatogens), each of which again divides without a resting stage into two spermatides (spermatoblasts). The four spermatides undergo various changes during which they become elongated, the nucleus, containing the chromatin elements, becomes the head of a spermatozoon and ends in a motile barb. The protoplasm of the cell-body is drawn out into a sheath through which the filament passes, and is continued beyond as the vibratile tail.

We have therefore this arrangement of parts in the male and female cells, to which for convenience of comparison I will apply these names.

I.	Primitive germ-cell.	=	Primitive sperm-cell.
II.	Two oocytes of which one forms the first polar body.	=	Two spermatocytes.
III.	The oocytes dividing into four oozoa, of which two are primarily functional in the parthenogenetic and one in the sexual egg.	=	The spermatocytes dividing into four spermatides, each becoming a spermatozoon, two of which may become reproductive in a male parthenogenesis, one is primarily functional in the sexual egg.

There seems little doubt that the chromosomes containing the germ-plasm of the species, are identical in the maternal and paternal reproductive cells, and that so long as their number is complete or sufficient to enable conjugation to take place, it is immaterial from which parent they may come. Boveri [1] succeeded in denucleating the egg of *Echinus microtuberculatus* and introducing spermatozoa of another species, *Sphaerechinus granularis*; when the egg developed, the larva was found to belong to the latter species, although living on the vitellus of the former. This was a case of male parthenogenesis. It however appears certain that one oozoon or spermatozoon requires conjugation with one other oozoon or spermatozoon before development can take place.

[1] Boveri, 'Ein geschlechtlich erzeugter Organismus ohne mütterliche Eigenschaften,' *Gesells. f. Morph. u. Phys.* München, July 16, 1883.

According to Weismann, the chromosomes are 'idants,' formed of smaller groups called 'ids'; these are made up of 'determinants,' which are again composed of 'biophors' or ultimate units. The biophors are more or less equivalent to the 'physiological units' of Herbert Spencer, the 'plastidules' of Haeckel, the 'gemmules' of Darwin, and the 'pangenes' of De Vries; although these variants are not exactly analogous to each other, they are all ultimate molecules of inherited plasm[1]. The nuclear thread is, so to speak, the web of the individual's destiny, and the ids which it contains are the inherited working plans of its architecture. As development advances, the ids are disintegrated into determinants, and the determinants into biophors, each group getting smaller until every biophor ultimately reaches and controls its own cell. The way in which the germ-plasm assumes the direction of ontogeny resembles a battalion marching to outpost duty. The main body steadily proceeds to distribute itself according to a predetermined plan; the battalion splits into half-battalions, the half-battalions into companies, the companies into pickets, and the pickets tell off their sentries, until each man at last finds himself at the post he has to guard. And just as a line of communication is always maintained through the battalion, so each nucleus is kept in touch with its cell, and each cell with the cells around it, by means of a fine protoplasmic reticulum which passes through the cell-walls[2]. It is obvious that influences affecting any stage of development must affect larger or smaller groups of determinants, just as any command given by an officer will

[1] Weismann, *Germ-plasm*, p. 41.

[2] Sedgwick, *Monograph of the development of Peripatus capensis*, p. 41.

affect the number of men particularly under him, and may alter their original course.

In cases of alternation of generations, and in those cases in which the two generations do not differ from each other in the full-grown condition, but in which the eggs develop differently, Weismann holds that there must be two kinds of germ-plasm, each containing the determinants of one form, and that these two must be passed separately along the germ-tracks, from one generation to another, so that each must always contain the other, stored away in an inactive condition [1].

In the case of gall-flies there is often a well-marked difference of structure between the females of the two alternating generations. The wing determinants in the winged *Trigonaspis crustalis* (Plate II, fig. 18 a) must have been modified in the wingless *Biorhiza renum*, (Plate II, fig. 18), but they appear again in *Trigonaspis crustalis*. It is improbable that lost determinants would be redeveloped in this way, and therefore there must be two alternating sets of determinants. These, Weismann holds, are contained within the same germ-plasm, but never become active at the same time [2].

I believe that in the function of the polar bodies we possess the simplest explanation of the problem of alternating determinants in the Cynipidae.

According to Weismann's earlier views [3], the first polar body removed ovogenetic nuclear substance which, after the maturation of the egg, had become superfluous and injurious; while the second polar body removed as many different kinds of idioplasm as were afterwards introduced by the sperm-nucleus.

He has abandoned this view of the function of the

[1] Weismann, *Germ-plasm*, p. 176. [2] Ibid. p. 178.

[3] *Essays on Heredity*, vol. i. p. 365, Oxford, 1891.

first polar body, and, according to his later views, the extrusion of both polar bodies is a provision for withdrawing promiscuously certain ids of germ-plasm for the purpose of securing variation. He says: 'I consider this remarkable and apparently useless process of the doubling and two subsequent halvings of the idants, as *a method of still further increasing the number of possible combinations of idants in the germ-cell of one and the same individual*[1]'; the three quarters of the mass of germ-plasm which passes into the polar bodies, he regards as being 'again lost[2],' while what is left in the ovum, after being increased by one spermatozoon, is halved by the first nuclear division; one half going to direct ontogeny, and the other half going to form the primary sexual cells: but as these last divide and behave at first like other somatic cells, they must, he thinks, possess active idioplasm as well as unalterable germ-plasm, and they must therefore contain more ids in their nuclear matter than do somatic cells[3].

I incline to the view that these cells in the Cynipidae remain somatic, and simply form the rudiments of the sexual organs, but that the function of the polar bodies is to provide the primitive reproductive cells. These bodies contain the inactive germ-plasm, historically prepared for this very purpose, and it is scarcely possible to imagine that nature would create this phylogenetic epitome of the species to be extruded as functionless, or to be broken up and again lost[4]. It is undeniable that they are of great value in promoting variation. The first division of the nucleus into two oocytes is not a reducing division, but results, so far as the germ-plasm is concerned, in two equivalent cells.

[1] Weismann, *Germ-plasm*, p. 247. [2] Ibid. p. 248.
[3] Ibid. p. 192. [4] Ibid. p. 248.

In the sexual egg, however, the second division follows immediately upon the first, and the extrusion of one oozoon reduces the chromosomes by half their number, which is again made good by those of one spermatozoon. While, therefore, in the parthenogenetic egg those 'material bearers of ancestral qualities' remain the same from generation to generation, they are changed in the sexual generation by each cross fertilization, and in this exists the advantage of amphimixis. For the evolution of species, individual variation is essential, and those individuals who derive half their germ-plasm from one parent, and half from another, each bringing in different lines of ancestors, must present greater variation than those who derive their germ-plasm from one parent and one ancestral line. Sexual reproduction is thus of advantage to the species in so far as it helps to increase inherent tendency to variation, and enables evolution to take place by the steady accumulation of slight beneficial differences[1]. The random withdrawal of the ids of ancestors by a species of lot, as laid down by Weismann, must be considered simply as a provisional hypothesis; and it seems, according to Prof. Hartog, that mathematically its effect, if it took place at all, would be the opposite of what Weismann expected[2].

Although the polar bodies were first noticed by Müller in 1848, their importance has only been recently appreciated. Balfour[3] considered their extrusion as the removal of part of the constituents of the germinal vesicle which are necessary for its functions as a complete and independent nucleus to make room for equivalent parts of the spermatic nucleus; and he con-

[1] Darwin, *Origin of Species*, p. 132.

[2] Prof. Hartog, *Nature*, vols. xliv and xlv, 1893.

[3] F. M. Balfour, *Comparative Embryology*, vol. i. p. 63, 1880.

sidered that the function of forming polar cells had been acquired by the ovum for the express purpose of preventing parthenogenesis. Van Beneden[1] and Minot[2] regard the polar bodies as male elements removed from a hermaphrodite cell. Bütschli, Hertwig[3], and Boveri incline to regard them as abortive ova and an atavistic reminiscence of primitive parthenogenesis. Geddes and Thomson[4] consider their extrusion due to the tendency of every cell to divide at the limit of growth, but favour the view that the process may be an extrusion of male elements. They consider, however, that these cells have no history, though they occasionally linger on the outskirts of the ovum, are seen to divide, and be penetrated by 'misguided' spermatozoa[5].

The homologous character of oozoa and spermatozoa has been pointed out, and these so far retain the habits of their protozoan ancestors as to require conjugation: in the parthenogenetic form, the two oozoa conjugate in each oocyte, in the sexual form one oozoon and one spermatozoon unite to form the fertilized ovum or oosperm, but I believe the three oozoa which form the polar bodies, unite together or conjugate with three spermatozoa, previous to that repeated division by which those bodies are prepared to be received as the earliest embryonic germ or sperm-cells into the rudimentary germ-tracks[6].

[1] E. Van Beneden, 'Recherches sur la fécondation,' *Arch. de Biologie*, iv, 1883.

[2] C. S. Minot, 'Theorie der Genoblasten,' *Biol. Centralbl.* ii. p. 365.

[3] O. Hertwig, *Die Zelle und die Gewebe*, Jena, 1892.

[4] Geddes and Thomson, *Evolution of Sex*, p. 107, 1892.

[5] Ibid. p. 105.

[6] H. Henking, *Zeitschr. f. wissensch. Zoologie*, liv. 89; V. Graber, 'Keimstreif der Insecten,' *Denkschrift d. K. K. Akad., Math.-Nat. Cl*, Wien, lvii, 1890.

The division of the primitive sperm-cell into four takes place in the seminal tubes, each fourth becoming subsequently a spermatozoon; while the corresponding division of the primitive germ-cell is that associated with the extrusion of the polar bodies. As soon as one spermatozoon enters the ovum, Fol describes the vitelline membrane as appearing to rise up, to prevent the entry of other spermatozoa into it. The polar bodies lie above this membrane, and between it and a thinner layer, so that even if this were the case, other spermatozoa are not hindered from reaching them. Spermatozoa in numbers are constantly seen entering the ovum, and especially the polar eminences.

In order to trace the disposal of the germ-plasm present in the nucleus, the egg of *Ascaris megalocephala* (*bivalens*) may be taken as the most thoroughly worked out. In it the primitive sperm-cell contains four chromosomes, which become doubled in the first spindle, after which the cell divides into two spermatocytes, each containing four chromosomes and their respective centrosomes. Each spermatocyte divides into two spermatides, and each of the four spermatides becomes a spermatozoon with two chromosomes. In the primitive germ-cell the four chromosomes become doubled in the first spindle, the nucleus divides into two (oocytes we may term them for convenience), one oocyte remains in the ovum with four chromosomes, and the other oocyte with its four chromosomes becomes the first polar body, which breaks up into two oozoa with two chromosomes in each. The oocyte remaining in the nucleus, without any resting stage, undergoes a second division into two oozoa: one oozoon containing two chromosomes is extruded as the

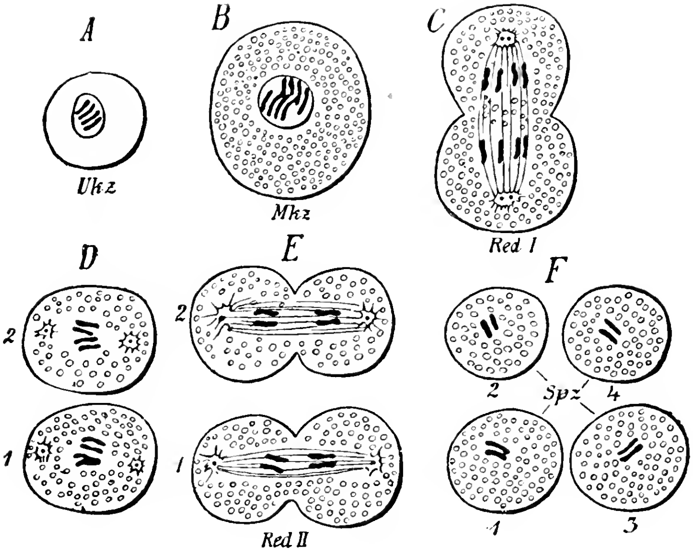


Fig. I.

Diagram of the formation of spermatozoa in *Ascaris megalocephala*, var. *bivalens*. (Modified from O. Hertwig.) *A*. Primitive sperm-cells. *B*. Sperm-mother-cells. *C*. First nuclear division. *D*. The two daughter-cells, or spermatocytes. *E*. Second 'reducing' division. *F*. The four grand-daughter cells, the sperm-cells, or spermatides, each becoming a spermatozoon.

To face p. xxviii.

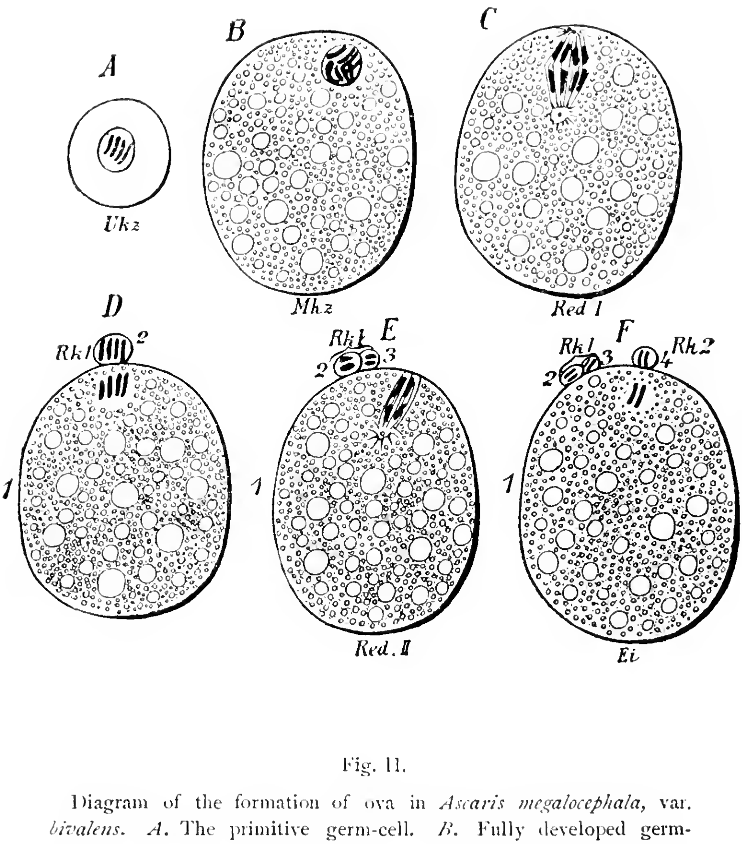


Fig. 11.

Diagram of the formation of ova in *Ascaris megalocephala,* var. *bivalens.* *A.* The primitive germ-cell. *B.* Fully developed germ-mother-cell, with chromosomes doubled. *C.* The first nuclear division. *D.* One daughter-cell (oocyte) extruded as the first polar body. *E.* The second or reducing division; the retained, and the extruded oocyte, dividing, and forming four grand-daughter cells (oozoa). *F.* The ripe egg-cell, the functional oozoon; the other oozoa, 2, 3, and 4, being the polar bodies.

second polar body, and one oozoon is left containing the remaining two chromosomes.

Assuming that the egg of one of the parthenogenetic species of Cynipidae had the same number of chromosomes as the species of Ascaris just described, four chromosomes would be extruded as the first polar body and four would remain in the nucleus. In that of a sexual species, on the contrary, six chromosomes would be found in the polar bodies and only two in the nucleus; but when fertilization took place, two chromosomes would enter the ovum with one spermatozoon, and six chromosomes would be added to the polar bodies when three other spermatozoa united with them. Thus the polar bodies of one egg of the parthenogenetic generation would contain four chromosomes available for the supply of germ-plasm to the next generation; while the polar bodies of a sexual egg would afford twelve chromosomes for the germ-plasm of the generation that follows. It is clear that if the polar bodies contain the germ-plasm of the next generation they must be fertilized by three spermatozoa, since in the sexual generation male and female characters are equally transmitted. If this be the case, we ought to find the eggs of the parthenogenetic generation much more numerous than those of the sexual, because the parthenogenetic germ-tracks have received the produce of twelve, while the germ-tracks of the sexual generation have only received that of four chromosomes; and it is to be presumed that the ova produced from them would bear something like this proportion to each other, if this theory held good. What are the facts? The summer sexual generations, whose germ-plasm has been received from the parthenogenetic polar body, produce from 200 to 400 eggs; while the winter agamous generation, which receives its germ-

plasm from the fertilized polar bodies of the sexual generation, produces from 1,000 to 1,200 eggs; or in an approximate proportion to the number of chromosomes postulated as present.

The impression which long prevailed that one spermatozoon was equal potentially to one ovum, led observers to regard the presence of more than one spermatozoon as an act of 'polyspermy,' as abhorrent to nature, and a cause of monstrosity[1]. But Kupffer, Benecke and others record the fact that spermatozoa do enter the 'peculiar protoplasmic protuberances,' many appearing to form pronuclei after gaining access to the ovum, so that in numerous species polyspermy appears to be the rule.

A great deal has recently been done in working out the development of the reproductive rudiment in insects, and it seems that the cells which become the ova, and which I believe to be chiefly those primarily set aside in the polar bodies with or without corresponding spermatozoa, can be traced to the rudiment of the germ and sperm-tracks of the embryo. These germinal track-cells, formed by the first segmentation, surround the primitive germ-cells to form with them the rudimentary reproductive organs. In the germogen one germ-cell and a nutritive circle of germinal epithelium cells form a cluster, and these grow forward together, the germinal epithelium growing in between each batch. In the upper part of the developing egg-tube, each batch is very small, but as it advances it increases steadily in size. In the egg-tube of the Cynipidae the egg-stalk curves round the next egg, and the clubbed end of the stalk gives the appearance of a large and small egg alternating.

In some asexual species of Hemiptera the oocyte,

[1] Selenka, E., *Befruchtung des Eies*, 1871.

which would become in an agamous species the first polar body, is not actually extruded but may be seen as a smaller cell lying close to the nucleus; and in some sexual eggs, both polar bodies are similarly retained.

It will be apparent how simply this view of the functions of the polar bodies in Cynipidae accords with the facts of alternating generations.

The fly which emerges from the gall of *Spathegaster baccarum* in June is sexual, and lays an egg which extrudes two polar bodies. The germ-plasm in these polar bodies after being united with that of three spermatozoa, is received by the embryo germ-tracks of this egg, and when from that egg the agamous *Neuroterus lenticularis* emerges in April, it is this germ-plasm which forms the nuclei of the ova contained in its tubes, consequently these ova can only reproduce the sexual flies of *Spathegaster baccarum.*

Again, the agamous *Neuroterus lenticularis* lays an egg which extrudes one polar body. The germ-plasm in this polar body is received by the germ-tracks of the embryo, and, when from that egg the sexual *Spathegaster baccarum* fly emerges, it is this germ-plasm which forms the nuclear matter of the ova and spermatozoa contained in its tubes, and consequently these ova and spermatozoa can only reproduce the agamous fly of *Neuroterus lenticularis.*

The two streams of germ-plasm are thus going on independently, and are each capable of acquiring and accumulating beneficial variations, so that the general dictum of Weismann is correct: 'the basis of the alternation of generations as regards the idioplasm, must, in all cases, consist of a germ-plasm composed of ids of at least two different kinds, which ultimately take over the control of the organism to which they give rise.' In

this way we have a means not only of securing variation, but of maintaining the fixity of species, which is equally important.

Alternating generations disappear as we ascend higher in the animal and vegetable scale, or as life lengthens beyond the period when seasonal alternation could be of advantage; then the purpose in view seems to be the approximation and assimilation of consecutive generations, and the continuous uniformity of the species. It is not quite clear how this result is attained, but the polar bodies cease to monopolize the transmission of the unalterable germ-plasm; probably another nuclear division, after fertilization and before ontogeny has begun, is added to them [1], and well marked atavism is only found as a pathological occurrence when the assimilating forces fail.

It is next of interest to inquire how the various structures of the gall came to be evolved. It may be taken as perfectly certain that the tree does not form them in a disinterested manner for the sake of the Cynips. Darwin says: 'If it could be proved that any part of the structure of any one species had been formed for the exclusive good of another species, it would annihilate my theory, for such could not have been produced through natural selection [2].' So far as galls are concerned, Darwin's theory is perfectly safe. The 'excitatory emanations,' as Professor Romanes [3] aptly calls them, which lead to gall-growth, can only have arisen by gradual and increasing improvements in the initial stages of their formation, acting through natural selection, over an unlimited period of time, and through numerous consecutive species

[1] Weismann, *Germ-plasm*, p. 192. [2] Darwin, *Origin of Species*, chap. vi. [3] Romanes, *Nature*, vol. xli. p. 80, 1889.

Galls may be arranged in groups of gradually increasing complexity, beginning with those like *Spathegaster baccarum*, and leading up to the complicated structure of *Cynips Kollari*. Beyerinck's classification following that of Lacaze-Duthiers, is into five groups:—

1. Simple galls, consisting of nutritive tissue enclosed in thin-walled parenchyma with vascular bundles:
   Neuroterus ostreus, Spathegaster albipes, S. baccarum, S. Aprilinus.
2. Galls similar to these, but having the nutritive tissue first enclosed in sclerenchyma, which forms an 'inner gall':
   Neuroterus lenticularis, N. laeviusculus, N. numismatis, N. fumipennis, Aphilotrix Sieboldi, A. autumnalis, A. radicis, A. globuli, Andricus curvator, Biorhiza renum, B. aptera.
3. Galls possessing an inner gall like the last, but having it surrounded by thick-walled parenchyma:
   Dryophanta longiventris, D. divisa.
4. Galls with the inner gall enclosed in a spongy layer of branched parenchyma, with wide intercellular spaces, and having the surface covered with a differentiated epidermis:
   Unilocular. *Dryophanta scutellaris.*
   Multilocular. *Teras terminalis.*
5. Galls which have the inner gall enclosed in thick-walled parenchyma, and then in spongy tissue; and which have a differentiated epidermis:
   Cynips Kollari.

Besides these histological differences, the outward characters are also of varying complexity; each infinitesimal improvement, which has been of service as a protection against parasites, or has been successful in securing natural conditions favourable to the life and

growth of the larva, has been preserved, and has formed the starting-point of further beneficial variations. It is always that larva which has been able to induce successful morphological abnormalities, which is reproduced to continue the race; the unsuccessful perish. The ruling force is natural selection; it is impossible that intelligence or memory can be of any use in guiding the Cynipidae; no Cynips ever sees its young, and none ever pricks buds a second season, or lives to know the results that follow the act. Natural selection alone has preserved an impulse which is released by seasonally recurring feelings, sights, or smells[1], and by the simultaneous ripening of the eggs within the fly. These set the whole physiological apparatus in motion, and secure the insertion of eggs at the right time, and in the right place. The number of eggs placed is instinctively proportionate to the space suitable for oviposition, to the size of the fully grown galls, and to the food supplies available for their nutrition. *Dryophanta scutellaris* will only place from one to six eggs on a leaf which *Neuroterus lenticularis* would probably prick a hundred times. The veins and petiole of the leaf carry onwards water and salts derived from the soil, and return the organic products of the leaf-cells; and these food currents render them desirable situations for gall-growth. The under surface of the leaf is folded outwards in the bud (vernation conduplicate), so that it is the first part reached, when buds are pricked. When expanded leaves are pricked, the spongy mesophyll of the under surface is much more easily penetrated than the upper surface, which is covered with the cuticle of an epidermis, that rests on closely

[1] Weismann, *Essays on Heredity*, vol. i p. 95.

packed palisade cells; the lower surface is consequently the situation most in favour.

Whatever form the gall takes, the potentialities of the tissue-growth exhibited by it, must be present at the spot pricked by the fly. It is not necessary to assume, with De Vries, that every vegetable cell contains the potentialities of every other cell in a latent condition. The conical growing point in every bud contains the germ-plasm of the next shoot, and consequently of the whole plant.

The potentialities of growth being present, they are called into activity by the larva, a result advantageous to the larva and sometimes described as disinterested and self-sacrificing on the part of the plant[1]. We have just seen that, so far as the larva is concerned, the peculiar structures of the gall owe their origin to their success in feeding and defending it; and so far as the plant is concerned, these structures have been evolved in consequence of their value in enabling the plant to repair injuries in general, and the injuries inflicted by larvae in particular. If John Doe raises a cane to strike Richard Roe, and Richard throws up his arms intuitively to parry the stroke, the action does not indicate a prophetic arrangement of molecules to frustrate John in particular, but an inherited action of defence. The first act of an injured plant is to

[1] St. George Mivart, *Nature*, Nov. 14, 1889. 'Now surely it is too much to ask us to believe that the germ-plasm of the plant, in the first instance, before even, say, a single cynips had visited it, had in the complex collocation of its molecules, an arrangement such as would compel the plant which was to grow from it, to grow those cells and form a gall.' And in a note he adds: 'It would be very interesting to know how natural selection could have caused this plant to perform actions which, if not self-sacrificing (and there must be some expenditure of energy), are at least so disinterested.'

throw out a blastem, and only those larvae survive to hand down their art, which emerge from an egg so cunningly placed as to excite the growth of a nutritive blastem. It is not always possible to keep the besiegers from using the waters of the moat, although there is no disinterested thought of the besiegers' wants when the ditches are planned. So in the war-game that goes on between insect and plant, natural selection directs the moves of both players, but there is nothing generous or altruistic on either side.

The means of defence against parasites which have been evolved by galls are many of them very curious. *Aphilotrix Sieboldi* and some others[1] secrete a sweet glutinous secretion which, like honey dew, is particularly attractive to ants, and leads them to act as sentinels in guarding the galls from parasites. Occasionally ants will go so far as to cover the secreting galls over with a concrete made of sand, leaving only a tunnel by which they pass up to reach the stores of honey dew.

A glutinous secretion is sometimes found on long tufts of hair growing from the gall. A defence of this kind is used by *Andricus ramuli*, and forms a stockade which entangles parasites before they reach the gall.

A layer of thick-walled parenchyma affords a protection to some larvae, such as *Dryophanta longiventris*; in others a thick layer of spongy parenchyma, as in *Teras terminalis*, serves the same purpose; in *Cynips Kollari* both these layers are present; and in addition, these and many other galls, have an inner gall of stony hardness which guards the larva like a shirt of mail.

[1] *Cynips glutinosa* glues small insects to the gall; and a sweet secretion is found on *Cynips calycis*, growing on *Q. pedunculata*. Giraud, *Verh. z.-b. Ges. zu Wien*, 1859; Dr. E. Ráthay, *Nature*, vol. xlv. p. 546, 1892.

Great size, as in *Aphilotrix radicis*, occasionally puts the larva beyond the reach of the parasite, while the very opposite condition protects by insignificance. Another effective protection is found in *Andricus curvator*, where the inner gall lies in a large hollow chamber, an arrangement which makes the work of the parasite difficult and uncertain.

Outside enemies such as tits, pheasants, and squirrels are as much to be feared as parasites. The larvae are defended from these, sometimes by the nature of the outer gall, which in *Aphilotrix fecundatrix* consists of closely imbricated scales resembling a hop strobile. In *A. Sieboldi* the outer gall is hard and stony; in *Cynips Kollari* and *Trigonaspis crustalis*, the tannin which is contained in the tissues renders them distasteful. As the galls mature the percentage of tannin becomes less, but the hardening of the epidermic layers which then takes place affords a new line of defence. After the gall has fallen another set of influences secure its safety by the changes they produce in its surface-colouring. The galls of *Andricus ostreus*, *Biorhiza renum*, and many others, are supplied, as Beyerinck has pointed out, with certain hydrocarbon compounds, which absorb moisture and undergo molecular changes after they reach the ground; with these chemical changes the growth of the larva and the development of protective coloration in the gall take place.

Cynips Kollari, *Dryophanta scutellaris*, and a few other gall-larvae and gall-flies, have the power of emitting a disagreeable bug-like odour, which is not sexual, since agamous species possess it, but probably protects the flies to some extent from birds. Certain galls have a fruity and aromatic smell [1], the use of which does not

[1] Paszlavszky, *Wien. Ent. Zeit.*, 1883. p. 130.

seem quite clear, unless they can be swallowed and voided undigested by a temporary host.

It is remarkable that characters, closely resembling those acquired by fruits, should have been evolved from a totally different cause. In the case of fruits these characters have been of service in securing the distribution of the seeds; in the case of galls, in securing the safety of the larvae; but in both cases it has been their fitness that has brought them into existence.

Darwin and all writers before him held that the force calling out gall formation was due to a chemical secretion injected by the gall-mother. Malpighi considered that it acted as a ferment on juices existing in the plant; and this was the view of Réaumur, but he added to it the thermal effect of the egg, and the nature and character of the wound, which varies according to the shape of the ovipositor of each species. Dr. Derham thought the formation was 'partly due to the act of the plant, and partly to some virulency in the juice or egg, or both, reposited on the vegetable by the parent animal; and just as this virulency is various according to the difference of its animal, so is the form and texture of the gall excited thereby.' Darwin speaks of galls as produced 'by a minute atom of the poison of a gall-insect,' and compares them to the specific local processes of zymotic diseases. Sir James Paget, writing in 1880, said that 'the most reasonable, if not the only reasonable theory, is that each insect infects or inoculates the leaf or other structure of the chosen plant with a poison peculiar to itself.' This may be taken as the view accepted by scientists[1], until in the following pages Dr. Adler showed conclusively that there was no foundation for supposing

[1] See 'Galls,' *Encyclop. Britann.* ed. 9, where the same view is expressed.

that the gall-mother injected any irritating secretion whatever, and Beyerinck [1] proved that the fluid ejected by the gall-fly is without taste or smell, and absolutely unirritating if injected under the skin. It is probably nothing more than a very mild antiseptic dressing applied to the wound made in the plant. Both these authors show plainly that it is not in the gall-mother, but in the larva, that we must seek for the cause of gall-growth; and that it is the nature of the salivary secretion, and the manner of feeding of the larva, peculiarities inherited by each species, which give the characteristic growth to the gall. The fact that sometimes a blastem has actually begun to form before the egg-shell has ruptured, proves that one of the exciting causes must be a chemical fluid, secreted by the salivary glands, and possessing amylolytic and proteolytic ferments. This fluid is capable of passing through the cell-walls and producing effects at a distance of several mm. beyond actual contact with the larva [2].

The necessity for the continuance of the excitation during the whole period of gall-growth is shown by its cessation when the larva has perished by parasites. In some galls, however, the parasites are evolving the power of prolonging gall-growth beyond the death of the gall-maker, although they have not yet actually acquired the art of initiating it.

The duration of gall-vitality is shortest in succulent galls, such as *Spathegaster baccarum*, *S. albipes*, *S. tricolor*, and *S. verrucosus*, growing from leaves; or such as *S. Taschenbergi*, *S. similis*, and *Trigonaspis crustalis*, growing from dormant buds. Galls which grow within the leaf substance, like *Spathegaster vesicatrix* and

[1] Beyerinck, *Über die ersten Entwickl. einiger Cynipidengallen*, p. 179.
[2] Hoffmeister.

Andricus curvator, live as long as those leaves of which they form part. *Aphilotrix fecundatrix* and *Cynips Kollari* die at the end of the first summer; *Dryophanta longiventris*, *Aphilotrix collaris*, *A. globuli*, *A. autumnalis*, and *Neuroterus ostreus*, perish during the first winter; the spangle-galls and *Biorhiza renum* live till spring; *Aphilotrix radicis*, *A. Sieboldi*, and *Biorhiza aptera* do not die till the second winter; while *Andricus inflator* may almost be termed perennial, since new oak-buds are developed upon it in the following year.

DESCRIPTION OF PLATES[1]

PLATE I.

Fig. 1. Galls of Neuroterus lenticularis.

Fig. 1ª. Galls of Spathegaster baccarum, on the leaf and flowering catkin.

Fig. 2. Galls of Neuroterus laeviusculus.

Fig. 2ª. Galls of Spathegaster albipes (× 2).

Fig. 3. Galls of Neuroterus numismatis, one gall enlarged.

Fig. 3ª. Galls of Spathegaster vesicatrix, one gall enlarged.

Fig. 4. Galls of Neuroterus fumipennis.

Fig. 4ª. Galls of Spathegaster tricolor.

Fig. 5. Galls of Aphilotrix radicis. One in the fresh state, the other in section, after maturity.

Fig. 5ª. Galls of Andricus noduli. One shoot bears the fresh galls, the other the galls of the previous year.

Fig. 6. Galls of Aphilotrix Sieboldi. On one stem the galls are fresh, on the other mature and woody.

Fig. 6ª. Galls of Andricus testaceipes.

Fig. 7. Galls of Aphilotrix corticis. One portion of the bark exhibits the fresh, the other the mature galls.

Fig. 7ª. Galls of Andricus gemmatus, showing the holes through which the flies have emerged.

Fig. 8. Galls of Aphilotrix globuli. The woody inner gall shown at maturity.

[1] The galls were drawn from fresh specimens by Herr O. Peters, Göttingen.

Fig. 8a. Galls of Andricus inflator. Section showing the inner gall chamber.

Fig. 9. Galls of Aphilotrix collaris. Fresh galls shown in the bud and detached. Mature adherent galls are also shown.

Fig. 9a. Galls of Andricus curvator on the leaf and twig. Section showing the inner gall.

Fig. 10. Galls of Aphilotrix fecundatrix, showing the inner gall detached.

Fig. 10a. Galls of Andricus pilosus (× 3).

PLATE II.

Fig. 11. Galls of Aphilotrix callidoma.

Fig. 11a. Galls of Andricus cirratus (natural size and × 3).

Fig. 12. Galls of Aphilotrix Malpighi.

Fig. 12a. Galls of Andricus nudus (× 2).

Fig. 13. Galls of Aphilotrix autumnalis, showing the mature gall detached.

Fig. 13a. Galls of Andricus ramuli.

Fig. 14. Galls of Dryophanta scutellaris.

Fig. 14a. Galls of Spathegaster Taschenbergi, at maturity after the escape of the flies. One fresh gall enlarged.

Fig. 15. Galls of Dryophanta longiventris.

Fig. 15a. Galls of Spathegaster similis. One on the twig, one showing through the bud, and one enlarged.

Fig. 16. Galls of Dryophanta divisa.

Fig. 16a. Galls of Spathegaster verrucosus. One on the leaf and one on the petiole. One on a leaf, and one escaping from a bud, enlarged (× 2).

Fig. 17. Galls of Biorhiza aptera. Fresh galls of the first year (experimentally grown); beneath, a mature woody gall.

Fig. 17a. Galls of Teras terminalis; the lower is a mature gall in section.

Fig. 18. Galls of Biorhiza renum, with the fly magnified.

Fig. 18a. Galls of Trigonaspis crustalis. Flies, male and female, magnified.

Fig. 19. Galls of Neuroterus ostreus.

Fig. 19a. Galls of Spathegaster aprilinus.

Fig. 20. Galls of Aphilotrix seminationis on the leaf and flowering catkin.

Fig. 21. Galls of Aphilotrix marginalis.

Fig. 22. Galls of Aphilotrix quadrilineatus.

Fig. 23. Galls of Aphilotrix albopunctata.

PLATE III.

All the figures in this plate are drawn from photographs. The egg when accompanying the ovipositor is drawn to the same scale. Ovipositors belonging to alternating generations bear the same numbers.

Fig. 1. Ovipositor of Andricus cirratus, $\times 55$. The terebra is withdrawn, that the two plates, the muscles, and the seta, may be more clearly displayed.

1–5. The five muscles described in the text as moving the terebra.

h. The posterior plate. *v*. The anterior plate. *b*. The arch. *c*. The horn. *s*. The seta. *p*. The anal papilla. *st*. The sheath of the terebra.

Fig. 2. Ovipositor of Neuroterus laeviusculus, with egg ($\times 30$).

Fig. 2ᵃ. Ovipositor of Spathegaster albipes, with egg ($\times 36$).

Fig. 3. Ovipositor of Neuroterus fumipennis ($\times 36$).

Fig. 4. Ovipositor of Aphilotrix radicis, with egg ($\times 25$).

Fig. 4ᵃ. Ovipositor of Andricus noduli, with egg ($\times 36$). The serrated spiculae are withdrawn.

Fig. 5. Ovipositor of Dryophanta scutellaris, with egg ($\times 30$).

Fig. 5ᵃ. Ovipositor of Spathegaster Taschenbergi, with egg ($\times 36$).

Fig. 6. Ovipositor of Biorhiza renum ($\times 36$).

Fig. 6ᵃ. Ovipositor of Trigonaspis crustalis ($\times 30$).

Fig. 7. Ovipositor of Teras terminalis ($\times 30$).

Fig. 8. Egg of Biorhiza aptera taken from the ovary direct; the adjoining figure exhibits one with the embryo ($\times 200$). The egg-stalk is cut short.

Fig. 9. Egg-tube from the ovary of Neuroterus fumipennis. Three eggs are seen in the course of formation ($\times 100$). In the last, which is the most developed, the formation of the egg-stalk is distinctly seen.

Fig. 10. Egg of Aphilotrix autumnalis, taken from a bud ten hours after oviposition ($\times 200$). The egg-stalk is shut off from the egg-cavity. Its whole length is not shown.

ALTERNATING GENERATIONS

IN

OAK GALL-FLIES

CHAPTER I.

INTRODUCTION.—EARLIER VIEWS.—FIRST OBSERVATIONS ON ALTERNATION OF GENERATIONS.—METHODS OF INVESTIGATION.

THE curious fact that in many species of oak gall-flies female specimens alone were found, long attracted entomologists to a closer study of this interesting family. But T. von Hartig[1] was the first to demonstrate by experimental breeding, after having reared many thousands of flies, that there are numerous species in which none but females exist; and that these when they emerge from the gall have their ovaries filled with perfectly developed eggs, which they at once proceed to deposit. Although the occurrence of parthenogenesis in these species had been placed beyond doubt by these experiments, there was much in the life

[1] *Über die Familien d. Gallwespen.* Germar's *Zeitschr. f. d. Entomol.* 1840-43, vol. ii. pp. 176-209; vol. iii. pp. 322-358; vol. iv. pp. 395-422.

history both of the agamous and of the sexual forms still left to be elucidated. There was no means by which this could be done satisfactorily except by direct experimental breeding. In carrying this out, however, many, practical difficulties occurred, as constantly happens in experiments of this nature, and these served for a long time to delay the solution of the problem; so for a season at least it was necessary to rest satisfied with a provisional explanation which was in reality little better than a simple hypothesis.

In the year 1861 an entirely new theory was propounded by Osten-Sacken [1], whose investigations into the history of the numerous species of North American oak gall-flies are well known to the scientific world. He believed he had discovered that those species which had hitherto been considered agamous were in reality sexual, but that the males were developed from differently formed galls. If this theory were correct all that remained to be done was to discover which were the associated gall-forms. But further observation did not confirm this view, and Osten-Sacken had to abandon it.

Some time afterwards, in 1864, Walsh [2], an American entomologist, advanced a totally different opinion. Walsh had obtained out of apparently exactly similar galls, on one occasion individuals of *Cynips spongifica* of both sexes, and on another occasion females only, but of *Cynips aciculata* which are quite different in form. Had this observation been correct, and had it been

[1] *Stettiner Entomolog. Zeit.* 1861, vol. xxii. pp. 405–423.

[2] Proceedings of the Entomological Society, Philadelphia, vol. i.

true that from the same gall there had emerged not only one male but also two different female forms, it would have been fatal to the theory of parthenogenesis in the agamous Cynipidae. All the agamous species would come at once to be regarded as dimorphous female forms, and it would only be necessary to ascertain which were the allied female forms. It looked as if we had here among the gall-flies a phenomenon analogous to that which Wallace had discovered among the Malay Papilionidae, where females of the same species are found of two or even three entirely different forms. Walsh's theory, however, received but little countenance, and in Germany it was refuted by Reinhard[1] who succeeded in establishing in the most satisfactory manner that parthenogenesis undoubtedly did exist among many species of Cynipidae. After this the subject seems to have dropped, and I am not aware of any researches, either in favour of or against the views of Walsh, having been made for a considerable time. Indeed it was not until 1873, after Walsh's death, that his fellow-countryman Bassett[2] published some fresh observations on the propagation of Cynipidae, of which the most interesting is the following:—Bassett had repeatedly found enormous numbers of a gall belonging to a species of Cynips, on a small oak (*Quercus bicolor*). These galls appeared with the leaves, causing shapeless swellings of the petiole and midrib; they contained

[1] Reinhard, 'Die Hypothesen über die Fortpflanzungsweise der eingeschlechtigen Gallwespen,' *Berl. Entom. Zeitschr.* 1865, vol. ix.

[2] *Canadian Entomol.* (May, 1873, vol. v. pp. 91–94).

a large number of larvae, and in June there emerged flies of each sex in nearly equal proportion. Late in the summer there was formed on the points of the young shoots of the same oak tree, a differently shaped gall in which the flies passed the winter. This latter species occurred in the female sex only. It closely resembled the former species, but was somewhat larger. From this observation Bassett arrived at the conclusion that each species of Cynips which is found occurring exclusively in the female sex is succeeded by another generation which is bisexual: and this he contended was entirely opposed to Walsh's hypothesis. Bassett concluded by saying that it would not surprise him if it were proved that every species of the genus Cynips had each year two generations differing in the manner indicated by him. Had I been acquainted with Bassett's work in the year 1875, when I began to investigate the Cynipidae more carefully, I should probably more easily have found the key to the mysterious problem of their propagation. A lucky chance led me to select the species of *Neuroterus* for my first experiments: these galls are easily collected in large numbers, and there is little difficulty in rearing the flies. In every case I made a point of breeding the flies from the galls, so that I might be absolutely certain of the species. The flies emerge in March and April from *Neuroterus* galls which had matured in autumn, and they proceed at once to lay their eggs in the buds of the oak. It struck me as remarkable that although the egg was laid so early, the gall did not develop until July: and it was the strangeness of this

circumstance, added to a desire to investigate the method of gall formation, that led me to undertake my first direct experiments in breeding. These afforded me the surprising result *that from the eggs laid by Neuroterus there appeared a totally different generation, one so wholly unlike its parent that it had been described hitherto as of another genus* (*Spathegaster*). This fact was published by me in 1877 [1], and what Bassett had only thrown out as a conjecture in 1873 was now proved and demonstrated in one species at least. It is not then correct to affirm that Walsh had previously discovered this alternation of generations. Walsh had only broached the theory that to one male form might belong two entirely different female forms which had until then been described as distinct species: but it is clear that the alternation of generations in the Cynipidae, as discovered by me, had nothing whatever in common with Walsh's supposed dimorphism. After I had once discovered this remarkable alternation of generations in *Neuroterus* it was interesting to investigate the propagation of the remaining genera and species. The fauna of this locality (Schleswig) includes about forty species, and this fairly represents the oak gall-flies of North Germany; to these therefore I steadily extended my observations. But before I go into any account of these species in detail, it may be well first to describe shortly the method which I adopted in carrying out my experiments.

In order that the results which I obtained might be unquestionable it was necessary to select a method

[1] *Deutsche Entomolog. Zeitschr.* 1877, Heft I.

which provided against every possible source of error. This could only be satisfactorily accomplished by watching the development of the gall of each species, from the time when the egg was laid until the gall reached maturity. Unfortunately, however, this peculiar difficulty exists, that the most important phase of development, viz. that during which the eggs of the fly are buried in the bud or tissues of the oak, must unavoidably be hidden from direct observation. Indirect observation alone is available, for any actual examination of the eggs when laid must necessarily end in their destruction. Thus if a gallfly lays its egg in a bud, one can predict with certainty what gall will be produced, so long as care is taken that the same bud is not pricked either before or afterwards by another fly. Breeding experiments must therefore be so arranged as to enable each species to be isolated and watched while actually depositing the egg.

For this purpose I had a quantity of little oak trees planted in numbered pots, each pot serving for experiments with flies of the same species. The experiments were made in a room, and the flies were carefully watched from the time they were placed upon the tree until they began to prick the buds: those buds which had been undoubtedly pricked were then marked by means of a thread tied around them. It was naturally impossible to go on watching the flies for many hours together, and I adopted the plan of covering the trees over: in this way flies placed on the trees were prevented from escaping, and at the same time those of other species were kept away. At first I used glass

protectors, but afterwards I found covers made of gauze and provided with a glass top were more suitable: they can easily be made of any size, are convenient for observation, and allow of free ventilation; besides under them a tree can be watched for days together, whereas a bell-glass protector soon becomes dimmed with moisture and requires frequent cleaning.

The oak saplings I have sometimes grown and sometimes obtained from nurserymen. The four to six year old saplings are to my mind the most convenient size, and a large choice of them makes experimental breeding much more easy. I employed almost entirely *Quercus sessiliflora*. It is essential that a sapling about to be used in an experiment should have its buds well developed, as these are always preferred by the flies. There is a difficulty in rearing species which only prick flower-buds, since young saplings which do not produce flowering catkins are useless for the purpose. The only way to rear those species is to make the experiments on full-grown trees in the open air, taking every means to guard against possible error [1]. On the other hand it is very easy to make experiments on saplings with species which prick the leaves or bark. Such briefly was the plan adopted by me in investigating the development of the species which I am about to describe.

As it is very difficult, and in some cases almost impossible, to distinguish the flies of nearly related species from each other, any illustrations of the insects

[[1] Dr. Beyerinck used for this purpose cubes of wire covered with muslin and tied round the branch.]

themselves would be practically useless. But all the species can be distinguished without difficulty by means of their galls, and these have been drawn as faithfully as possible from fresh typical examples. The galls of associated generations have been marked in the plates by the same number, the generation occurring only in the female sex being marked thus, '1,' and that in which both sexes occur thus, '1^a'.

For greater convenience of reference, I have arranged the species in the following groups:—

I. NEUROTERUS.
II. APHILOTRIX.
III. DRYOPHANTA.
IV. BIORHIZA.

CHAPTER II.

DESCRIPTION OF THE SPECIES OF CYNIPIDAE OBSERVED, WITH A VIEW TO DETERMINING THEIR ALTERNATION OF GENERATIONS.

I. NEUROTERUS GROUP[1].

1. Neuroterus lenticularis. Ol.[2]

Gall. The gall appears on the under surface of the oak leaf, and occurs frequently in large numbers, forty to fifty on one leaf. It is circular, 4-6 mm. in diameter; the under surface which is in contact with the leaf is smooth and flattened, and of a whitish colour; the upper surface has a slightly conical prominence in the centre, and is of a pale yellow or reddish colour with brown stellar hairs. The galls appear in July, mature in September, and fall to the ground at the end of September or beginning of October. (Fig. 1.)

Rearing the Fly. The mature galls are collected at the time when they begin to detach themselves from the leaves. The larva, which may be seen lying in a small cavity in the centre of the gall, is still very minute and requires a certain degree of moisture for its further development. The galls should therefore be

[[1] *Neuroterus*, Hartig; *Spathegaster*, Hartig; *Ameristus*, Foerster; *Manderstjernia*, Radoszkowsky.

[2] *Cynips lenticularis*, Olivier; *Neuroterus Malpighii*, Hartig, Tasch., Thoms.]

laid on damp sand, but the airiest possible situation must be chosen, to avoid mildew. If the galls are kept in a room, the larvae develop much more quickly than they do in the open air, in consequence of the higher temperature, and in the course of about four weeks they are fully grown. Then if the galls are prevented from shrivelling, by keeping them on damp sand or over water, the first flies may be obtained in about four weeks more. In this way I have hatched flies in November and December, but it was soon apparent that these premature specimens were little fitted for experimental breeding. They were much weaker and more puny than those developed under natural conditions, and it is consequently preferable to leave the galls to pass the winter in the open air. This may very simply be done in the following way. Half fill a flower-pot with earth or sand, spread the galls upon this, and cover them over with a layer of moss. Then for greater protection tie a piece of gauze firmly over and plunge the pot up to its rim in the ground. This method of wintering is to be recommended for all galls, as they are thus placed under natural conditions, and it is certain that the development of the flies is left to follow its normal course. In this experiment the flies emerged mostly in April, but a few not until May. For this variation in the time of their appearance I believe that temperature is alone responsible.

Fly. Size 2·5–3 mm. Colour black; thorax dull, rough and finely punctate; abdomen shining; almost round when looked at from the side, somewhat compressed. Legs lighter; of a brownish red colour,

except the coxae and the base of the femora which are brown. The antennae are fifteen jointed, the first two joints being yellowish.

Experimental breeding. My earliest attempts at breeding on a large scale were made in 1875 with *Neuroterus lenticularis.* These experiments are easy enough with this species if only a sufficient number of flies are available. As soon as they leave the gall they begin to deposit their eggs in the oak buds.

It had hitherto been taken for granted that this species produced a gall resembling that from which it emerged; many points nevertheless remained obscure and puzzling. It had been long known for example that the gall of *Neuroterus lenticularis* did not appear until July, but as the eggs were deposited by the flies in April, three months must have passed away before any trace of gall formation had become visible. It was assumed therefore that the embryonic development of the larva demanded this lengthened period; and this was quite possible, since other species seemed to require an incubation of even longer duration. For example *Andricus curvator* emerges in June and lives for two or three weeks during which it lays its eggs, but the galls do not appear until early in the following year. This could only be explained by supposing that the egg remained dormant during the winter, and did not develop until next spring, as is known to be the case with the eggs of many butterflies. The three months' egg-rest of *Neuroterus lenticularis* therefore was not unprecedented. More conclusive evidence in support of this supposition was wanting; but even if it were correct it failed to explain another

phenomenon. We sometimes find on a single oak leaf from 100 to 150 *Neuroterus* galls, therefore there must have been the enormous number of 100 to 150 eggs laid in a single bud; and these eggs must have been accurately deposited on the rudimentary leaf while it was yet folded in the bud. This was a supposition that seemed very improbable.

My breeding experiments soon threw a flood of light on these apparently mysterious phenomena.

In the year 1875, as soon as a sufficient number of flies had emerged from the galls, I began in March to place them on the oak saplings and watched to see them prick the buds. I was soon able to satisfy myself as to how a fly proceeds when it deposits its eggs. It first examines the buds carefully with its antennae until it finds one that suits it, when it takes up a different position. It advances towards the apex of the bud and pushes its ovipositor down under one of the bud-scales. After several attempts the ovipositor is forced in and glides down under the bud scales to the base of the bud-axis which it penetrates from without inwards. This can only be accomplished by imparting to the ovipositor a direction at an obtuse or right angle to the course it followed when entering. The natural curvature of the ovipositor here stands the fly in good stead, but it requires a vast expenditure of time and strength before it can penetrate the heart of the bud. In order to investigate satisfactorily the various steps constituting the act of ovipositing, it is a good plan to fix the fly in the very act by dipping it into chloroform or ether.

During my experiments in 1875 one oak sapling had

thirty-four buds pricked between March 28 and April 6. Of these buds only nineteen developed, and as they unfolded and their leaves became visible I examined their surfaces with the greatest care for any sign of the eggs which had been deposited in the bud. I was at first unsuccessful, but after a long search I discovered at last five of the young shoots exhibiting traces of gall formation on their leaves. They were small round excrescences, rich in sap, which grew tolerably quickly, and were soon recognizable as the galls of *Spathegaster baccarum*.

Thus in spite of taking every precaution to ensure that the buds were pricked by *Neuroterus lenticularis*, a perfectly different gall had been formed from the one out of which this *Neuroterus* had emerged. I did not rest satisfied with this one attempt, but continued for many years to make experiments with this and many other species of *Neuroterus*.

It is remarkable in experimental breeding how small is the number of galls that actually develop compared with that of the eggs deposited in the buds. Many of the buds themselves come to nothing, but even in those which grow there are a great number in which the galls do not form. For example in 1877 I made an experiment in which the results were particularly unfavourable. An oak was pricked abundantly by *Neuroterus lenticularis*, and yet only a single *Spathegaster baccarum* gall was formed. In such experiments it very probably happens that the conditions of life natural to the flies have not been successfully reproduced, and consequently many of the eggs laid fail to develop. I have, however,

observed the same thing happen when oaks growing in the open air have been pricked, and I am therefore compelled to attribute to meteorological conditions a most important influence over the development of the egg. The appearance of the flies almost always takes place about the same time, and embryonic development begins immediately after the eggs are laid. Absolute rest in the evolution of the egg never occurs, for even if the temperature should be very low the formation of the blastoderm begins at once. Naturally this proceeds more slowly in a cold than in a warm season. I have satisfied myself by various experiments that when pricked buds are kept in a warm room the several stages of embryonic development run their course much more quickly than they do in buds kept in the open air. In any case the embryo reaches its full development in a few weeks. It may happen, however, that at the particular time when this takes place vegetation may be backward, and the circulation of the sap may not yet have begun in the tree, nevertheless the time when the development of the embryo is completed is just the time when gall formation should make a beginning. As long as the embryonic envelopes remain intact gall formation does not begin, but it starts the moment the larva frees itself from the egg coverings. Around the larva cell proliferation now commences and this corresponds to the first beginning of gall formation. But the production of this cell proliferation is conditional, and depends on the state of vegetable growth; the sap, the pabulum of which the cells are formed, must be in circulation. When cold weather retards

vegetation so that the bud gets little or no nutritive material, gall formation cannot begin and the larva perishes. Accordingly we find in a cold and late Spring the galls of those flies which prick buds early are very sparingly found. It happened, for example, that the Spring of 1877 was cold and very late, and the early galls were unusually scarce. This interfered with experimental breeding and made my investigations exceptionally difficult. If in every case where a bud had been pricked by a gall-fly, a gall could be unfailingly collected, then it would be easy to prove the succession of the several generations; unfortunately, however, many of these experiments fail.

In order if possible to guard against this, I had the oaks which had been pricked brought into a warmer room, so as to force them to shoot; but even then I was scarcely more successful. In some species certainly the development of the galls was hastened, but in others on the contrary the results were negative only.

[The Common Spangle is found on *Quercus pedunculata*, *Q. sessiliflora*, and *Q. pubescens*.

Inquiline. *Synergus Tscheki* in April.

Parasites. *Eurytoma signata*, *Torymus auratus*, *T. hibernans*, *T. sodalis*, *Syntomaspis fastuosus*, *S. caudata*, *Pleurotropis rosarum*, in May. *Pteromalus dissectus*, *P. tibialis*, *Decatoma biguttata*, *Pezomachus gallarum*, *Pleurotropis sosarmus*, *Entedon flavomaculata*, and *Megastigmus dorsalis*.]

1a. Spathegaster baccarum[1]. L.

Gall. Spherical, 3–5 mm. in diameter; of a greenish colour, often studded with small red spots; of soft,

[[1] *Cynips quercus-baccarum*, Lin.; *Spathegaster interruptor*, Hartig; *Neuroterus lenticularis*, sexual form, Cameron; *Neuroterus baccarum*, Mayr.]

sappy consistence; the gall grows through the leaf, its larger segment projecting from the lower surface of the leaf. This gall not only occurs on the leaves but is found also on the peduncles of the male catkin, and is then smaller and of a pale reddish colour. (Fig. 1 a.)

Fly. Size, 3–5 mm.; of a black colour; thorax dull, slightly rough; legs and coxae yellow, as also the basal segments of the antennae. Abdomen distinctly pedunculate. The male has fifteen, the female fourteen joints to the antennae. The wings are long, broader towards the tip, and longer than the body.

Rearing the Fly. The fly emerges from the beginning to the middle of June. Owing to the sappy nature of the galls it is not wise to collect them too long before the flight time of the fly, otherwise it is difficult to prevent the galls from shrivelling and drying. In order to hatch the flies satisfactorily it is absolutely essential to keep the galls fresh: it is scarcely possible to do this for longer than eight days in closed tin or glass vessels. Since these flies occur in both sexes it is necessary to see that they copulate before ovipositing. I have been in the habit of spreading the galls out on damp sand as I collected them, and placing over them a gauze covering. The males are usually the first to appear, and as soon as the females emerge fecundation takes place, but generally too rapidly for this to be actually observed. To demonstrate that it has occurred it is necessary to prepare the *receptacula seminis* of some of the females for microscopical examination. If these are found filled with spermatozoa it may be taken as

probable that most of the females of the brood have been fertilized, and breeding experiments may be proceeded with.

The female flies are then placed on oak saplings, care being taken that the leaves are tender and in actual growth, as it is only in that condition that they can be pricked. Unless leaves in this state can be provided, no results need be expected.

I made my first observations on ovipositing in *Spathegaster baccarum* in the open air. In the year 1875, from June 18 to 21, I watched many of the females creeping about on the tender oak leaves and pricking them on the under surface. Having marked the pricked leaves by tying a thread around the leaf-stalk, I waited for the development of the galls. In about three weeks the beginning of gall formation was observable, and the galls could soon be recognized as those of *Neuroterus lenticularis.*

In June, 1876, I placed flies, reared by myself, on an oak sapling and repeated this same experiment under more exact control. Two leaves were pricked, and at the end of twenty days I recognized the first beginning of gall formation, and the galls again proved to be those of *Neuroterus lenticularis.*

Now the mystery was completely solved, and I had discovered what became of the eggs laid in the buds by *Neuroterus lenticularis*, and why the galls appearing in July are found in such numbers on a single leaf.

[The currant gall is found in May on *Quercus pedunculata*, *Q. sessiliflora*, and *Q. pubescens.*

Inquilines. *Synergus albipes* in May and June. *S. facialis* and *S. radiatus* in June. *S. apicalis*, *S. ruficornis*, *S. thaumacera.*

Parasites. *Torymus abdominalis*, *T. incertus*, *T. regius*, and *T. auratus* in May and June. *Eurytoma rosae* and *Pteromalus immaculatus* in July. *Tetrastichus atrocaeruleus*, *Eupelmus annulatus*, and according to Barrett the *Tortrix*, *Zeiraphera communana*.]

2. Neuroterus laeviusculus. Schenck [1].

Gall. Cup-shaped, the edges thinned and incurved; in the centre there is a small but distinct boss surrounded by a circle of brownish hairs; diameter 2–3 mm. The form of the gall is often irregular, the rim bent; colour pale or reddish. The gall appears in July and matures in September. (Fig. 2 [2].)

Rearing the Fly. When the mature gall falls from the leaf, its under surface will be found to be distinctly swollen. In order to observe the development of the flies indoors the galls must be kept on damp sand. Their progress may be forced, and in a room they will emerge in November, but in the natural course they do not appear until March of the following year. The earliest date on which I have found them in the open air was March 9.

Fly. Size, 2–4 mm.; black; thorax smooth and shining; abdomen much compressed, elongate; legs distinctly paler, white or yellowish, coxae and base of femora dark.

Experimental breeding. I have made experiments in breeding with *Neuroterus laeviusculus* in the same

[[1] *Neuroterus pezizaeformis*, Schtdl.]

[2] This gall is frequently confused with that of *Neuroterus fumipennis*. I myself made this mistake, and in my earlier publications these two names must therefore be transposed, but the facts remain unaffected.

way as with the former species, and have frequently succeeded in getting the flies to prick the small oaks. The first accurate experiments were made in March, 1875. Between March 14 and 26, thirty-six buds in all were pricked by a large number of flies. On the unfolding leaves there appeared in May the gall of a totally different fly, *Spathegaster albipes.* From the strict control exercised there could be no doubt that these galls proceeded from *Neuroterus laeviusculus.* From my first experiment I obtained thirty-six galls, but from others made in 1877 I only got two galls. As a rule experiments made with these flies are pretty certain to succeed.

[The smooth spangle gall is found on *Q. pedunculata.*

Inquiline. *Synergus Tscheki* in April.

Parasites. *Torymus sodalis* in March and April. *T. hibernans.* The spangle galls live about nine months.]

2^a. Spathegaster albipes. Schenck [1].

Gall. Size, 1–2 mm. in length; oval with a short apical point, of a greenish yellow colour, smooth or thinly set with solitary hairs. The galls are sessile on the leaves, which they deform more or less, causing indentations or sinuosities and often stunting them in their growth. This is due to the mode of origin of the gall which is formed on the rudimentary leaf while yet in the bud. The area occupied by the gall in the bud is of course small, but the effect upon the leaf when it expands is much more marked. (Fig. 2^a.)

Fly. Size, 1–2 mm. long; black; thorax smooth

[[1] *Neuroterus laeviusculus,* sexual form, Cameron. *Neuroterus albipes* Mayr.]

and shining; abdomen distinctly pedunculate. Legs pale, only the coxae and bases of the femora dark. The flies emerge at the end of May or beginning of June.

Experimental breeding. I observed these flies for the first time on June 3, 1875, while they were busy in the open air pricking the under sides of the tender oak leaves. They are very delicate little flies, and can only be kept alive for a few days, but it is not difficult to observe them ovipositing if they are provided with very tender leaves. They are first seen to move about actively and examine the under surface of the leaves carefully with their antennae. They then direct the point of the abdomen perpendicularly to the surface of the leaf, the terebra is pushed into it, and an egg glides down into the channel thus pierced. This fly can deposit a large number of eggs in the leaf in a short space of time. The first traces of gall formation are found at the end of three weeks as little hairy spots which soon develop into the galls of *Neuroterus laeviusculus*. Of these there may be as many as 200 on a single leaf.

[Schenck's gall is found in May on *Quercus sessiliflora* and *Q. pedunculata*.

Inquiline. *Synergus apicalis*.]

3. Neuroterus numismatis[1]. Ol.

Gall. Very pretty circular galls, like buttons covered with brown silk, with a shallow depression in the middle. Diameter, 2 mm. They mature in the autumn with the preceding (*Neuroterus*) gall. (Fig. 3.)

[[1] *Cynips numismatis*, Oliv. *Neuroterus Réaumuri*, Hartig.]

The flies are reared in exactly the same way as *Neuroterus lenticularis.*

Fly. 2–5 mm. in length; black; thorax dull, finely punctate; scutellum somewhat closely haired. The colouring of the legs variable, yellowish brown, bases of the femora mostly dark. Abdomen, looked at from the side, almost round; basal joints of the antennae dark, which is the only character by which this fly is distinguished from *Neuroterus lenticularis.*

Experimental breeding. Experiments, in the manner described above, were also made with this fly, the first being in March, 1875. From this first attempt, in which thirty-two buds were pricked, I obtained in all five galls which were formed under the leaf surface and proved to be those of *Spathegaster vesicatrix.* In 1876, I repeated the experiment with the same result. Later also an English entomologist Fletcher [1] obtained from similar experiments the same species of *Spathegaster.*

[The silk button spangle galls appear in July on *Quercus sessiliflora*, *Q. pedunculata*, and *Q. pubescens.*

Inquiline. *Synergus Tscheki*, March to June.

Parasites. *Torymus mutabilis*, June—August, *T. inconstans*, *T. fuscicrux*, *T. geranii* in July. *Platymesopus tibialis* in June. *Eurytoma curta*, *E. aethiops*. *Pteromalus domesticus* in July. *Eupelmus urozonus*. *Pleurotropus sosarmus*.]

3a. Spathegaster vesicatrix. Schltdl.[2]

Gall. These galls are inconspicuous and are embedded in the substance of the leaf, which they resemble. They project only slightly above the level of the surface.

[1] J. E. Fletcher, *Entom. Month. Mag.*, vol. xiv. p. 265 (May, 1878).

[[2] *Neuroterus numismatis*, sexual form, Cameron. *Neuroterus vesicatrix*, Mayr.]

Each bears in its centre a little conical projection from which rays run out to the margin of the gall. (Fig. 3[a].)

The flies emerge in June, and are very easily reared if the galls are collected shortly before they mature.

Fly. Size, 2 mm.; black; thorax shining; legs yellowish, coxae and bases of femora dark. Male and female similar.

Experimental breeding. As it is very difficult to collect the flies of this species in large quantity, I have only once been able to make an experiment in breeding, and that was in the open air. On June 20, 1875, I observed several females creeping about on the under surface of the oak leaves and laying their eggs. I marked eight leaves which had been pricked, by tying threads upon them. After three or four weeks small round galls appeared which proved to be those of *Neuroterus numismatis.*

[The blister-gall occurs in May on *Quercus sessiliflora* and *Q. pedunculata.* A different but similar gall appears on *Q. pubescens* and *Q. cerris.*

Inquiline. Sp.? of *Synergus.*

Parasites. Sp.? of *Torymus.* This gall continues to live after its gall-maker has emerged.]

4. Neuroterus fumipennis. Htg.[1]

Gall. Generally circular, with the edges often incurved and emarginate. The gall is of a pale or reddish colour with delicate brown stellar hairs. (Fig. 4.)

This gall has a certain resemblance to that of *Neuroterus lenticularis,* but has more frequently been

[[1] *Spathegaster varius,* Schenck.]

mistaken for *Neuroterus laeviusculus.* Indeed, as I have already said, I myself at the outset confounded *laeviusculus* with *fumipennis.*

Rearing the Fly. The galls are collected when they mature in the beginning of October, and are preserved through the winter in the same way as *Neuroterus lenticularis.* In one point however they differ essentially; in *lenticularis* the development of the larva begins and continues without intermission from the time the galls fall to the ground, but in *fumipennis* on the contrary there is a complete winter rest. If a gall of *fumipennis* be opened in the month of March, the larva will be found to be absolutely at the same point of development that it had reached in the autumn; whereas in the other *Neuroterus* galls the larva is by that time fully grown or has even assumed the pupa-state. It is only during the month of March that larval development begins in *fumipennis,* towards the end of April it becomes a pupa, and the perfect insect appears in May. But the actual date of its appearance varies from two to three weeks according to the temperature. It is not possible with this species, as with the others, to hasten the development of the larva by keeping the galls in a warm room during the winter months.

Fly. This fly is easily distinguished from all the other species of *Neuroterus.* Size, 2 mm.; thorax dull, black; base of abdomen orange; legs, including the femora, orange; wings, especially at the tips, smoky.

Experimental breeding. When the fly makes its first appearance in May it finds the oak buds already well developed and beginning to swell, while the scales

are becoming less tightly imbricated. It is thus comparatively easy for it to insert its terebra into the bud. I made my first experiments in May, 1875, and I repeated them in May, 1876. They are very active little flies, and in this respect differ from the former species; they are continually running from side to side and flying from one shoot to another. When the buds begin to loosen, they are able without much effort to insert their terebra and deposit their egg. It often happens that several eggs are deposited on the same leaf, while later we find from three to five galls growing there, and the leaf distorted and puckered. The gall produced by this species is that of *Spathegaster tricolor.*

[The cupped spangle gall is found in August on *Quercus pedunculata* and *Q. sessiliflora*; occasionally on the upper surface of the leaf
Inquiline. *Synergus Tscheki* in March of second year.
Parasite. *Torymus sodalis.*]

4a. Spathegaster tricolor. Htg.[1]

Gall. Soft and sappy; of a pure white or slightly greenish yellow colour; round, somewhat flattened at the summit, covered with simple upright white hairs, which usually fall off when the gall is mature, and it is then liable to be confused with *Spathegaster baccarum.* (Fig. 4a.)

The gall does not mature until July, and the fly emerges from the beginning to the middle of July.

Fly. Size, 2 mm.; black; thorax slightly shining, somewhat punctate; legs reddish yellow; abdomen dark brown, reddish yellow at the base; wings cloudy,

[[1] *Neuroterus tricolor,* Mayr.]

particularly at the tips; basal joints of the antennae pale; male and female similar.

Experimental breeding. I made, in 1875, some observations on the manner in which this species pricks the buds. On July 17 I found several females busily hunting about on the under surfaces of the oak leaves which they finally began to prick, and during the month of August the galls of *Neuroterus fumipennis* developed on the pricked leaves. I have not made any further experiments with this species.

[The hairy pea gall is found in June on *Quercus pedunculata* and *Q. sessiliflora*.

Inquilines. *Synergus albipes, S. facialis*, and *S. thaumacera* all in June and July.

Parasites. *Eurytoma rosae* and species of *Torymus* and *Pteromalus* in July. This gall is often found on Lammas shoots.]

The *Neuroterus* and *Spathegaster* forms just described had formerly been considered as belonging to different genera, because it was not known that they were alternate generations of the same insect. This view was perfectly justifiable since very important differences exist between the two generations. A comparison of the galls of the two generations would not lead us to associate the two species with each other, for the difference between them is often much greater than between two wholly distinct species, such as *Neuroterus lenticularis* and *Neuroterus numismatis*. I will refer later to the important distinction that the flies in the one generation belong to both sexes, and in the other exclusively to the female sex. The parthenogenetic propagation of *Neuroterus* is constant, and is now so satisfactorily established that it requires no further proof.

If we compare the flies of the two generations belonging to any of the species above described, we shall find the differences at first sight very slight. The difference of colouring is unimportant, and is chiefly observable in a slight variation in the colour of the legs; nor is the size of the body very different, while the form and surface markings agree in many points. At the same time it is not difficult to distinguish the one generation from the other, indeed if the two were placed side by side it would be difficult to mistake them, their bodily conformation being totally different. The *Neuroterus* is more compressed, the abdomen much more developed, the wings shorter than the length of the body, the antennae about two-thirds of the latter. The *Spathegaster*, on the contrary, is more slender, has longer and narrower wings, which always exceed the length of the body; the antennae are somewhat less than two-thirds of the length of the body; and lastly the abdomen is not so strongly developed. The configuration and size of the abdomen depend entirely on the size and form of the ovipositor. When the ovipositor is of great length, as in *Neuroterus laeviusculus*, it lies in repose spirally coiled in the abdominal cavity; and from the greater space which such an ovipositor requires, a larger abdomen becomes necessary. In *Spathegaster*, the alternate generation, the ovipositor is totally different, being small and slender; and since it occupies little room within the body we naturally find the abdomen altered in form. This difference in the form of the ovipositor is a constant one, even when the two generations are otherwise much

alike. Thus for example *Neuroterus fumipennis* and *Spathegaster tricolor* resemble each other so much in size and colouring, that from a superficial examination they might easily be confounded ; but if we take into consideration their whole structure, the form of the abdomen, the length and shape of the wings, and lastly the ovipositor, the difference between the two generations is found to be sharply defined.

I will return hereafter to the consideration of the interesting variations in the ovipositor, on account of the importance of that organ. The principal forms exhibited in the illustrations (Plate III) are accurately drawn from photographs, so that the various details will be found given in their proper relative proportion.

As the two generations, just described as species of *Neuroterus* and *Spathegaster*, belong to the same insect, I felt strongly inclined to drop the usual practice of designating them as of two genera ; but I have retained these names, for the present at least, in order to avoid confusion.

In the earlier descriptions of these two genera the number of joints in the palpi were used as distinctions between *Neuroterus* and *Spathegaster*. In *Neuroterus* the maxillary palpi were said to be four-jointed and the labial palpi two-jointed: and in *Spathegaster* they were said to be respectively five and three-jointed. But a closer examination of these forms has convinced me that the maxillary palpi have invariably four, and the labial palpi always two joints.

II. Aphilotrix Group.

The genus *Aphilotrix* includes a large number of gall-flies among which I have been able to establish a similar alternation of generations. Like *Neuroterus* the genus *Aphilotrix* is found only in the female sex.

5. Aphilotrix radicis. Fbr.[1]

Gall. The gall is many-chambered, occurs on the roots and lower part of the trunk, and varies in size from a cherry to a man's fist. At first the gall is pale, almost pure white when formed underground and excluded from the light, and in consistence it resembles a potato. Later it becomes brown and woody until it is perfectly hard especially at its base. When it reaches maturity the upper surface has a fissured and uneven appearance and is of a brownish or black colour. On section it shows innumerable round larva chambers. (Fig. 5.)

Rearing the Fly. The mature galls which are found in the autumn are collected and kept through the winter in a cool place. The flies are perfectly developed in autumn, as may be proved by opening some of the cells, but they winter in the gall and do not emerge until the following spring, about the end of April or beginning of May.

Fly. Size, 5–6 mm.; reddish brown; the mesonotum is marked by three darker longitudinal stripes, one median and two lateral, and there is also a transverse

[[1] *Cynips radicis*, Fbr. *Andricus radicis*, Mayr.]

line in front of the scutellum; further the metathorax, and an irregular blotch on the first segment of the abdomen, are also dark, as well as the bases of the coxae and tibiae of the hind legs, and the claws. The thorax is closely covered with silky pubescence: the antennae are variously coloured, but the basal four joints are reddish brown, and the apex dark.

Experimental breeding. After the flies quit the galls they usually rest a few days before beginning to lay their eggs. When I first made experiments with this species in 1875 I expected them to select the roots or the lower part of the trunk to lay their eggs in, but I soon discovered that they always creep up the trunk in search of the buds. After they have carefully examined the buds with their antennae they begin to prick them. They do this just as it is done by a *Neuroterus*, but the fly takes up its position nearer to the base of the bud. It drives its terebra under one of the bud scales until it reaches the foot of the bud-axis. Thence it directs the channel not towards the centre of the bud, in which lie the rudimentary leaves, but below this point, and the tip of the terebra thus enters tissues from which later shoots are developed. Some eggs may, it is true, come to lie upon the base of the rudimentary leaves, but the greater part will be found lower down, and there are usually no galls found on the leaves themselves.

When the buds that have been pricked begin to shoot, a long interval takes place before there is any sign of gall formation. The earliest symptoms recognizable are a delay in the development of the bud,

and the presence of more or less deformity and swelling. A section through the parts exhibits little larva cells lying in the swelling. From my first experiments in breeding in 1875 I obtained undeniable evidence that those galls which had hitherto been described as belonging to *Andricus noduli* were produced by *Aphilotrix radicis.* In the following year I repeated the same experiment with the like success; indeed this species commends itself to the experimentalist, for with it failure hardly ever occurs.

As a rule *Andricus noduli* galls lie within the shoot, but occasionally they are found in the petiole, because, as I have already observed, the eggs of *Aphilotrix radicis* sometimes come to lie within the range of the rudimentary leaves. It is worthy of remark that occasionally specimens of *Aphilotrix radicis* appear very late, at the end of May or the beginning of June. By this time the buds have expanded before they are pricked by the flies, consequently a large quantity of eggs are laid in the same shoot, giving it the appearance afterwards of being perfectly covered with little *noduli* galls. From such a distorted shoot, scarcely an inch long, sometimes as many as 200 flies will emerge. It is hardly possible that so large a number of eggs could have been laid in an unexpanded bud.

[The truffle gall occurs in September on *Quercus sessiliflora*, *Q. pedunculata* and *Q. pubescens.*

Inquiline. *Synergus incrassatus* which forms larva chambers around the gall maker.

Parasites. *Torymus nobilis*, *T. crucarum*, *T. amoenus*, *T. radicis*, *Pteromalus quercinus*, *Tetrastichus quercûs*, *Eurytoma rosae.*]

5a. Andricus noduli. Htg.[1]

Gall. The gall is scarcely 2 mm. long, and lies within an oak-shoot of that year's growth, but is often only recognizable from without by small round elevations of the bark. The mature galls form hollow cavities in the substance of the wood, lined with thin membranes. They are not unfrequently found in the leaf stalks, which then appear thickened and swollen. They give rise to more or less deformity (see Fig. 5a).

Rearing the Fly. To obtain the flies with certainty the shoots on which the galls are formed should not be collected too long before the flight time, otherwise the wood is apt to become too dry. The time when the flies emerge is variously stated, but I have convinced myself by many experiments that they begin early in August and go on to the middle of that month.

It may, however, happen that a few flies do not appear until the next year, these may come from late individuals of *Aphilotrix radicis*, but in any case they are a small minority.

Fly. Size, 2 mm.; males and females differ in colouring.

Female. Thorax black, dull, sometimes streaked with orange; abdomen orange with a black blotch on the back of the first segment; the tip of the abdomen and ventral sheaths black. Legs testaceous, the hind coxae dark; antennae dark, at the base testaceous.

[[1] *Andricus trilineatus*, Htg. *Andricus radicis*, sexual form, Cameron.]

Male. Thorax and abdomen black, the latter particularly shining; legs light, dirty yellow, the coxae and hind tibiae somewhat darker; antennae dark, pale at the base.

Experimental breeding. After a sufficient number of specimens have emerged from the galls, a certain interval must be allowed to elapse to make sure that the females are fecundated. When satisfied by the examination of the *receptaculum seminis* of several females that they have been fertilized, the experimental breeding may proceed. On account of the small size of the fly, it is better to continue the experiments on the same tree on which the galls grew. Care must be taken, however, to see that the flies can reach the roots easily. In order to secure this I planted several oak saplings in pots, with the long woody root turned up again towards the surface, so that the extremity protruded from the earth near the trunk. Even if the extreme point were to die off, lateral rootlets would form so near the surface that the flies could easily reach them. On an oak arranged in this manner I made an experiment on August 18, 1878. I was soon able to satisfy myself that several of the flies, after exploring the surface of the rootlets with their antennae, had finally pierced the root cortex with their ovipositor. A subsequent examination of the pricked spots revealed several eggs lying in the cambium layer.

The number of eggs laid at one spot varies greatly as shown by the size and number of larva cells in the later *Aphilotrix radicis* galls. I believe it frequently

happens that two or more flies lay their eggs close to each other at the same spot. I cannot conceive how otherwise the colossal compound galls sometimes found could be formed. On one occasion I collected 1,100 flies from one *Aphilotrix radicis* gall; as, however, a single *Andricus noduli* fly only carries about 500 eggs in its ovarium, it is clear that such a gall could only be produced by the co-operation of several flies.

On the little oak tree pricked in August, 1878, I was able to watch the subsequent development of the galls. In September a thickening of one of the pricked spots gradually took place, the bark was raised and at last broken through, and a new structure, of a hemispherical form, was obtruded. When, in October, vegetation ceased and the leaves began to fall, the growth of the gall stopped, but only to resume its course next spring. In this first stage of its growth the gall had the consistence of a potato, and sections could easily be made for the purpose of microscopical examination. The apparently homogeneous tissue was found to be studded with countless minute larva chambers. In the centre of each of these chambers lay a very small larva surrounded by a succession of concentrically arranged cells. The cells next the larva were the largest, were filled with starch granules, and some were undergoing degeneration. The cells of the more remote layers became steadily smaller until they finally passed into the surrounding cambium tissue. Here and there vascular bundles pushed their way into the newly formed stroma, and brought it thus into closer connexion with the parent tissue from which it grew.

About May the larva was fully developed, and the gall, which had finished its growth, had become woody.

In the course of the summer each larva passes into the pupa state; in the autumn the perfect flies are found, but they pass the winter within the galls, and only emerge in April of the next year.

It is remarkable that two years are required for the completion of this generation cycle. A certain proportion of the *Aphilotrix radicis* generation emerges in April of the first year, and the remainder in April of the second year; in the interval we have the sexual generation and the prolonged larval stage of *Aphilotrix radicis* itself.

[The knot gall is found in June on *Q. pedunculata*, *Q. sessiliflora*, and *Q. pubescens*.

Inquilines. *Ceroptres arator* in May and June of the second year: *Sapholytus connatus*, *Synergus apicalis* in May and June of second year: *S. vulgaris*.

Parasites. *Megastigmus dorsalis* and *Pteromalus quercinus*. This gall is often found on Lammas shoots.]

6. Aphilotrix Sieboldi. Htg.[1]

Gall. The galls are usually thickly aggregated on slender oak twigs, or on young trees, most frequently close to the ground. They are conical, and when fresh are covered with a beautiful cherry-red rind. They are found thus in June, but in the autumn when the galls are mature, the sappy outer rind dries, withers and drops off. Then the woody inner gall appears, like a firm cone, with regularly formed ridges running from

[[1] *Cynips Sieboldi*, Htg. *C. corticalis*, Schenck. *Andricus Sieboldi*, Mayr.]

the apex of the gall to its base. The tissue of the gall penetrates deeply into the wood of the oak and the smaller stems often die in consequence of this encroachment. (Fig. 6.)

Rearing the flies. The fly is very easy to rear if the mature galls are collected in the autumn and kept through the winter in a cool place. Next spring, at the end of April or beginning of May, the flies begin to leave the galls.

Fly. Size 4–5 mm. almost uniformly reddish brown; the front of the thorax is marked by some fine black lines, the metathorax is somewhat darker. Legs uniformly reddish brown. The whole thorax very hairy. Antennae dark, pale at the base. The fly is very like *Aphilotrix radicis* but rather lighter in colour.

Experimental breeding. It is not difficult to watch the fly while ovipositing. It behaves like *Aphilotrix radicis*, and the buds are similarly pricked, the fly pushing its ovipositor into the base of the bud-axis. The eggs, however, are usually placed in the area of the rudimentary leaves, and galls extremely like those of *Andricus noduli* are formed in the stalks and veins of the leaf. These have hitherto been described as *Andricus testaceipes*. To make sure, and to avoid confusion with the *Andricus noduli* galls, I have for several years made experiments in breeding, invariably keeping the little oak trees under strict control in a room; but I have always obtained the same galls, resembling the galls of *Andricus noduli*.

[The red barnacle gall is biennial, living about fourteen months, and is found on *Quercus sessiliflora* and *Q. pedunculata*.

Inquiline. *Synergus incrassatus.*

Parasites. *Torymus nobilis, Eurytoma rosae* and *Olinx trilineata.* These galls are attacked frequently by Tits and have the larvae picked out.]

6a. Andricus testaceipes. Htg.[1]

Gall. In many cases the galls are only recognizable by a round or tumid thickening of the stalks and veins of the leaf. (See illustration, Fig. 6a.) Within this thickening lies the gall, a hollow chamber scarcely 2 mm. long, separated by a thin membrane from the surrounding tissue: but this gall also occurs inside the wood of the shoot, and it is then impossible to distinguish it from the gall of *Andricus noduli.* The flies emerge, like *Andricus noduli,* at the beginning of August.

Fly. Size about 2 mm. *Female,* thorax black and dull, abdomen orange, back of the abdomen and ventral sheath dark, legs orange. *Male.* Entirely black, abdomen shining, legs pale yellow. This species cannot be distinguished with certainty from *Andricus noduli.*

Experimental breeding. If the number of flies be sufficiently large it is not difficult to observe them ovipositing. The fecundated females betake themselves for this purpose to the slender shoots or stems, and pierce the bark close to the ground. As a rule the eggs are laid in a ring within the bark of the selected shoot. Gall formation begins in the course of September. The bark at the pricked spots becomes thickened, and soon rises above that of the uninjured parts. If thin tranverse sections are made through the thickened portions, spherical masses of cells are seen in the

[[1] *Andricus Sieboldi,* sexual form, Cameron.]

cambium layer, with a central chamber in which the larva lies. At the beginning of the cold weather gall formation is arrested, to be resumed and rapidly completed in the following spring. In May the thickening of the bark increases very much, distinct roundish swellings are formed, which burst and disclose the beautiful red conical galls. They grow 4–5 mm. above the level of the bark, and their bases are rooted in the substance of the wood. In June they reach maturity, and in autumn the fly is fully formed, but passes the winter in the gall[1].

[The leaf-vein gall is found in June on *Q. sessiliflora.*
Inquilines. *Synergus apicalis* and *Ceroptres arator.*
Parasite. *Megastigmus dorsalis.*]

7. **Aphilotrix corticis.** L.[2]

Gall. These galls are found in the bark of thick oak roots, or in the swellings that form around old injuries to the bark, like those usually seen where boughs have been sawn off. When fresh the gall appears of a hemispherical or oval form, covered by a sappy, reddish yellow, or ochrey envelope. The real larva chamber lies under the level of the bark and penetrates by conical points into the substance of the wood. The bell-shaped upper half dries after maturity and falls

[1] These, like other galls, are greatly exposed to the attacks of various parasites (species of Torymus and Synergus), and it is interesting to observe how the gall has indirectly evolved a means of protection. The red sappy envelope secretes a sticky fluid which is eagerly sought after by ants, and that they may enjoy this nectar undisturbed, they build with sand and earth a perfect dome over the galls, and in this way provide the inhabitants with the best possible protection against their enemies.

[[2] *Cynips corticis*, Hartig. *Andricus corticis*, Mayr.]

off, presenting then quite a different appearance, and disclosing the base of the gall sunk in the bark. It is surrounded by a sharp somewhat raised rim which bears on its inner side a row of uniformly pierced punctures. These little openings belong to an earlier period of growth; and through them passed the vascular bundles that nourished the upper sappy half of the gall. Subsequently the fly gnaws the hole by which it emerges in the centre of the base. (Fig. 7.) The method of rearing and time of appearance are the same as in the other species of *Aphilotrix*.

Fly. Size 4 mm., the whole insect dark, of a brownish black colour. Margins of the orbits, base of the antennae, ventral keel and legs bright reddish brown; apex of femora paler as a rule. Thorax dull, covered with silky hairs.

Experimental breeding. These flies are easy to rear. Soon after they leave the galls they begin to prick the buds, giving a preference to those buds which have already begun to shoot. They push the ovipositor so deeply into the bud that the eggs are deposited on the base of the leaf germs. It might naturally be supposed that from their great resemblance to the two previous species a similar gall would be formed, and at first I expected to find a gall like *Aphilotrix Sieboldi*, but the experiments which I made in 1877–1879 satisfactorily cleared the matter up. Between May 6 and 8, 1877, twenty buds on a little oak tree placed in a room were pricked by *Aphilotrix corticis*. When in June the oak was in full leaf, I noticed here and there on a leaf-stalk, or in the axil

of a leaf, little greenish or brown elevations about 1 mm. high. As it happened I obtained no flies, for I had overlooked the time when they emerge and had allowed it to pass; all I could vouch for was, that by the beginning of August the flies had left the galls. In 1878 I repeated the experiment; between April 23 and 28, ten buds were pricked; and between May 3 and 6, twelve buds on a second oak. In June the same little galls appeared, from which the flies emerged at the end of July. In 1879 I made the experiment for the third time with similar results.

[The bark gall is found in September on *Quercus sessiliflora*, *Q. pedunculata* and *Q. pubescens*.

Inquiline. *Synergus incrassatus*.

Parasite. *Torymus corticis*.]

7a. Andricus gemmatus. n. sp.[1]

Gall. These galls are small and inconspicuous, scarcely 2 mm. long, and they are often overlooked because their apices are frequently the only parts that project. They are usually formed in the axil of a leaf, near the later winter buds, and apparently spring from the rudimentary bud. They are also sometimes found free on the shoots. It is possible that the egg is sometimes laid exactly in the axil of the later leaves, and this may give the gall the appearance of growing out of a little axillary bud. The gall consists of a thin smooth rind which at first is green but later of a brownish colour; and it can be recognized most easily by the hole through which the fly has emerged. (Fig. 7a.) Neither gall nor fly has been hitherto

[[1] *Andricus corticis*, sexual form, Cameron.]

described. I have chosen the name from *gemmare*, to bud, because the galls at first resemble little buds.

Fly. Size 2 mm. long. *Female*, black; thorax dull, sparsely haired; abdomen very shining, the ventral keel reddish brown; legs orange, coxae and posterior tibiae dark; antennae orange at base, apex dark. *Male*, black; abdomen very shining; legs somewhat paler, coxae and femora dark; base of antennae pale. They emerge at the end of July and beginning of August.

I have been unsuccessful in carrying out experimental breeding with this generation of *Andricus*, on account of the small number of flies I have been able to collect, and I could not therefore follow directly the formation of the *Aphilotrix corticis* gall. Besides, it is very difficult to get suitable oaks for such experiments, because these flies lay their eggs exclusively in tumid thickenings of the bark.

[The bud gall is found on *Q. sessiliflora* in May and June.]

8. Aphilotrix globuli. Htg.[1]

Gall. This beautiful green globular gall does not burst from the bud until September, and its base is then closely surrounded by bud-scales. When fresh the gall is covered by a sappy green rind, underneath which is the woody inner gall, with a large larva chamber. In October the gall falls out of the bud, the sappy rind is loosened and the woody inner gall left bare. But if the galls be collected when fresh, the green rind dries on, and shows an uneven reticulated surface, according with the description which we often

[[1] *Cynips globuli*, Htg. *Andricus globuli*, Mayr.]

find given of this gall. The woody inner gall is marked by regular furrows and ridges. (Fig. 8.)

Rearing the fly. There is some difficulty in rearing this fly because of the long duration of the larval state. Although the larva is full grown by the end of October it does not enter the pupa state that year. The statement that the flies appear in the following spring is founded on error. The larva state continues into the next year, and it pupates in the autumn, and the fly appears in the April following. But if the galls, when collected, are not kept as much as possible in the same condition as if in the open air, it is very difficult to rear the flies. The galls must therefore pass the winter in the open air in the way previously described, and it is only by this means that the larva can be got to undergo its metamorphosis successfully. If the galls are kept in a room the metamorphosis does not take place. I have kept galls with fully developed larvae for several years without obtaining a single fly. From the galls which pass the winter in the open air the flies as a rule emerge in the second, but in some cases not until the third year. Thus from the galls which I collected in October 1876, I obtained the flies in April 1878, but some did not emerge until April 1879. The same peculiarity occurs with several other species which I shall describe later.

Fly. Size 4 mm. long, head and thorax black, dull, thickly haired; abdomen very shining, dark above, reddish brown below; antennae dark throughout; femora reddish brown, but the coxae and tibiae of the middle and hind legs infuscated.

Experimental breeding. The flies emerge very early, some even by the end of March. On March 30, 1878, I made the following observations. Five pricked buds were carefully marked by threads tied round them. When pricking the flies behaved in a similar way to the species of *Aphilotrix* previously described. The ovipositor was again directed under the bud-scales and pushed on towards the base of the bud, so as to place the eggs not in the germs of the leaves but below them, and tolerably accurately in the centre of the bud-axis. Only one egg was laid in each bud, and each separate act required about twenty minutes. I naturally expected from this that out of each pricked bud only one gall would develop. The five pricked buds began to shoot in May; one, however, lagged in growth, and showed obvious signs of thickening. It soon became apparent that this was due to gall formation, and it afterwards developed the gall described as *Andricus inflator*. I only obtained one gall from this experiment. In the following year I repeated the attempt. On March 25, 1879, several flies were put upon a little oak and among them they pricked nine buds. In May I obtained two galls of *Andricus inflator*.

[The globular gall is found in September on *Quercus sessiliflora* and *Q. pubescens*.

Inquilines. *Neuroterus parasiticus*, *Synergus ruficornis* in July of second year, *S. nervosus* and *S. vulgaris*.

Parasites. *Torymus regius; Siphonura chalybea; Megastigmus dorsalis*, *Eurytoma rosae*, *Eupelmus azureus* (probably hyper-parasitic).]

8a. Andricus inflator. Htg.[1]

Gall. This gall is developed from a bud, is of a green colour, and has a foliaceous covering. In appearance it resembles an enormously thickened and shortened shoot. In the first year growth is not perceptibly interfered with, and the winter buds are formed in the ordinary manner above the gall in the axils of the leaves. Next year, however, all these shoots die away. A longitudinal section exhibits a cylindrical cavity within the gall, at the lower end of which there is a little inner gall-chamber from which the fly proceeds. The upper end of the cavity is closed by a covering which is at first red and later of a yellowish colour. (Fig. 8a.)

To collect the flies the galls must be gathered in the middle of June. The flies emerge at the end of June or beginning of July.

Fly. Size 2·4 mm. Head and thorax black, slightly shining; abdomen in the *female* black above, red or orange beneath; in the *male*, entirely black; legs orange, but the posterior tibiae and coxae dark; antennae dark, pale at the base.

Experimental breeding. The females as soon as they emerge and have been fecundated seek out the most tender buds, either terminal or axillary, and lay one egg in each bud. Sometimes the flies also prick those axillary buds which have been formed on the gall, and from these pricked buds the *Aphilotrix globuli* galls develop in September. In this way the singular fact

[[1] *Andricus globuli*, sexual form, Cameron. *Cynips inflator*, Thoms.]

is easily explained that an *Andricus inflator* gall is often found super-imposed on one or more *Aphilotrix globuli* galls. I have only made observations on *Andricus inflator* in the open air, and have not been able to make any more exact attempts at breeding.

[The twig gall is found in May on *Quercus pedunculata* and *Q. pubescens.*

Inquiline. *Sapholytus connatus.*

Parasites. *Megastigmus dorsalis, Torymus auratus, Decatoma Neesi, Pteromalus dissectus* and *P. Erichsoni.* The gall often exhibits buds upon it in the following year, and is perennial as regards its growth. The fly has the mesonotum uniformly shagreened, twelfth and thirteenth joints of antennae longer than broad, mesopleura striated.]

9. Aphilotrix collaris. Htg.[1]

Gall. These galls are easily overlooked from their small size. They are formed upon a bud, and when ripe are so deeply concealed within the bud-scales that only the apex of the gall can be perceived. They are conical, of a reddish brown colour when fresh, and from the base of each there springs a slender appendage which penetrates deeply into the axis of the bud. In September or October the gall becomes loosened and falls to the ground, and the appendage shrivels up and falls off, but very often we find galls remaining in the buds which on further examination prove to be adherent to them; hence the assertion that this gall passes the winter in the bud. But it has been proved that only inquilines or parasites are reared from those adherent galls: we have an instance in this of what is frequently found to be the case, that when an inquiline

[[1] *Cynips collaris*, Htg. *Andricus collaris*, Mayr.]

lays its egg in an immature gall, the growth of the gall is altered with the death of the original larva, and becomes pathological. Sometimes these morbid galls remain small, at others they become firmly rooted into the parent tissue. (Fig. 9.)

Rearing the fly. The same precautionary measures must be taken as in the former species of *Aphilotrix* in order to obtain the flies from the galls. The duration of the larval state is the same. After the galls are mature, a year and a half passes before the appearance of the flies.

Fly. 3 mm. long. Head and thorax dark, often with reddish lines on the back; thorax smooth and shining; scutellum reddish brown, dull, and hairy; abdomen dark, base sometimes reddish; legs orange; coxae always dark, and sometimes also the bases of the femora.

Experimental breeding. This fly has hitherto passed as rare, chiefly because the galls are difficult to find, and the rearing does not always succeed. Further observation has shown me, however, that in some years it is very common. I made my first attempts at breeding in 1876 with two flies, which pricked several buds between April 4 and April 6. The eggs were always laid in the rudimentary leaves in the centre of the bud, and accordingly it proved, as might have been expected, that the galls developed on the leaves. As soon as the buds had unfolded, a tumid thickening was observed on two of the leaves. This was the beginning of a gall which was soon recognizable as *Andricus curvator.* I repeated the experiment in 1878, putting six flies on a little oak, the buds of which they continued to

prick for several days. The result was convincing, as in June the little oak was perfectly covered with the galls of *Andricus curvator.* The illustration was taken from a shoot of this oak.

[The collared bud gall is found in August or September on *Quercus sessiliflora.*

Inquilines. *Synergus nervosus* and *S. pallieeps.*

Parasites. *Eurytoma verticillata* and *Syntomaspis caudatus.*]

9a. **Andricus curvator.** Htg.[1]

Gall. The gall forms on the leaves, and appears in May as an irregular thickening of the leaf surface. At first it presents, when cut through, a solid kernel, but as time goes on a cavity is gradually formed, and from its inner wall projects a small brown central gall. If several galls are formed on the same shoot, the leaves are hindered in their development, and remain rudimentary. The flies emerge in June.

Fly. Size 1·5 to 2 mm. Black. Thorax smooth, sometimes rather rugulose, without sculpture; abdomen black and shining; legs testaceous; coxae always, and femora often, dark. Males and females similar.

Experimental breeding. I have made many experiments with this species. If the fecundated females are placed on an oak sapling, as a rule they soon begin to prick the buds. To do this the fly perches on the point of the bud, and bores its ovipositor obliquely downwards into the interior. Only one egg is laid in each bud, and a long time elapses before any gall formation can be seen. The gall begins to develop in September, but occasionally as early as August. At first the gall is

[[1] *Cynips curvator*, Thoms. *Andricus perfoliatus*, Schenck.]

difficult to recognize, as its brown point scarcely shows beyond the scales of the bud, but when mature it projects more distinctly, and its base is gradually loosened from the tissues of the bud-axis. Before it was known that *Aphilotrix collaris* and *Andricus curvator* were alternating generations, it was supposed that the egg laid by *Andricus curvator* in June rested in the bud until the next year, and that then, when the period of growth returned, *Andricus curvator* galls were formed once more on the leaves. This was all the more easy to believe, because the bud in which the egg was laid in June, rests until the next year as a winter bud, and does not naturally develop in the same year. We see, however, in this, as in other cases, that a dormant bud may be induced to shoot by the larva.

[The curved leaf gall is found in June, and sometimes on Lammas shoots, on *Quercus pedunculata, Q. sessiliflora* and *Q. pubescens.*

Inquilines. *Synergus albipes, S. apicalis, S. facialis, S. radiatus* and *S. thaumacera* in June of the same year; and *Periclistus Brandti.*

Parasites. *Torymus auratus, T. abdominalis, Pteromalus cordairii, P. tibialis, P. meconatus, P. Saxesenii, P. dissectus, P. Erichsoni, P. jucundus,* in June and July of the first year; *Eurytoma gracilis,* in August; *Entedon sciancurus, E. cecidomycarnus, Eulophus laevissimus, E. metallicus, Siphonura viridiaenea, Mesopolobus fasciiventris, Telenomus phalaenarum, Decatoma biguttata, D. Neesi, Eurytoma rosae, Syntomaspis dubius, Pleurotropis metallicus, Elachestus petrolatus,* and *Eupelmus annulatus.* The larva chambers of the Synergi are usually near the surface and do not interfere with the gall-maker.]

10. Aphilotrix fecundatrix. Htg.[1]

Gall. This gall, which resembles a hop, is surrounded by closely imbricated scales, at first of a green colour,

[[1] *Cynips gemmae,* Lin. *Cynips fecundatrix,* Htg. *Aphilotrix gemmae,* Mayr, Fitch. *Andricus fecundatrix,* Mayr.]

but brown later; these then loosen and fall off. At the base of the cone there is a small inner gall of an elongated oval form, which at maturity becomes detached and falls to the ground. At first this inner gall is firmly adherent to the bud-axis, but in August this adhesion gives way owing to the contraction of the base, by which the scales are compressed more tightly together until they finally thrust the inner gall completely out. In this state the gall is of a yellowish green colour, and still of a soft consistence. The period of full maturity is reached on the ground, when the whole gall becomes dark, very firm, and hard, affording the larva ample protection against the influence of the weather. It is to be noted that galls sometimes remain concealed among the scales of the outer gall. (Fig. 10.) In many cases in a well developed outer gall, the inner gall may turn out to be small, round and rudimentary. These galls are found to contain one or more inquiline larvae, lying in separate loculi, and it is through their influence that normal development has been stopped and perverted.

Rearing the Fly. Although the gall is very common it is difficult to rear the fly successfully, for the larval state is very prolonged, and it is not easy to maintain the natural conditions of life during that period. The wintering must take place in the open air. The larva lies dormant as long as that of *Aphilotrix collaris*; I only obtained the flies in April 1878 from the galls collected in August 1876, and the flies of some galls did not emerge until the third year. If the galls after being collected are kept in a room, the metamorphosis of the

larva does not proceed; it may remain alive in the galls for several years, but at length it dies. In what way the alteration of the environment acts it is difficult to tell, but the operation of such atmospheric influences as cold, damp and heat appears to be absolutely necessary to secure the regular progress of metamorphosis. The flies emerge in April.

Fly. Size 4–5 mm. The whole fly dark, almost black; thorax dull, rugose, with white silky hairs; abdomen black and shining, but the sides more or less reddish brown; legs dark as a rule, the knees distinctly reddish brown, front legs at the widest part sometimes bright reddish brown, the upper part of the femur dark.

Experimental breeding. In conducting experiments with this species I have had some difficulty because the fly only lays its eggs in male catkin buds. As the little oak trees which I planted in pots produced no flowers, there was nothing to be done but to watch the flies ovipositing in the open air. I succeeded, on April 14, 1878, in accurately observing several of them while in this act, but to be quite clear about their manner of ovipositing, I allowed some flies reared by myself to pierce branches which I had cut off and brought indoors for the purpose. I found that the fly directed its ovipositor under the bud-scales until it pierced an anther, when it laid the egg in it. It was therefore certain that the gall would be formed on the anther. During my observations made in the open air, several buds were pierced under my own eyes, and I marked these by tying a thread around them. When

the male flowers developed in May following, delicate little galls could be seen on these pricked buds, situated either singly, or several together, on the pedicels of the flower. I found the same galls on two different trees, both of which had been pricked by *Aphilotrix fecundatrix.* I therefore felt satisfied that no mistake or deception was possible. The galls, about to be described, were evidently those of a species of *Andricus.* It is to be observed that the *Aphilotrix fecundatrix* pricks by preference, and perhaps exclusively, the flower buds of *Quercus robur* (*pedunculata,* Ehrh.). The reason for its preferring this species of oak is probably because it flowers about fourteen days earlier than *Quercus sessiliflora.*

[The artichoke or hop gall is found in July on *Quercus sessiliflora*, *Q. pedunculata*, and *Q. pubescens.*

Inquilines. *Synergus melanopus, S. evanescens, S. apicalis, S. vulgaris, Aulax fecundatrix.*

Parasites. *Eurytoma signata, Syntomaspis caudatus, Torymus regius* (*Callimome inconstans*), *Megastigmus dorsalis, Mesopolobus fasciiventris, Olinx trilineata,* and *Entedon leptoneurus.* The moth *Carpocapsa juliana* in the outer gall.]

10ª. Andricus pilosus. n. sp.[1]

So far as I know this gall has not hitherto been described. I have selected the specific name 'pilosus' because it is covered with short hairs and these serve to distinguish it from similar species.

This elegant little gall is about 2 mm. in length, of an elongated oval form, with a prominent apex, thin-walled, green at first but when mature of a brownish colour, covered with pale stiff hairs. The galls are found

[[1] *Andricus fecundatrix*, sexual form, Cameron.]

among the anthers on the catkins either singly or several together. (Fig. 10[a].) In order to rear the flies, the galls should be gathered in the end of May shortly before they are mature, and the flies are then obtained about the beginning or middle of June.

Fly. 1·5 mm. long; black; thorax smooth, slightly shining, scutellum rugose; abdomen uniformly black, shining; legs from the coxae to the lower third of the femora uniformly dark, the remainder yellowish-testaceous; antennae yellowish, the apices fuscous. The male has the same colouring but the antennae are almost wholly dark.

Experimental breeding. I made a series of experiments with this species in June, 1878, both indoors and out. In some cases I brought the fly straight to the oak sapling, and in others I tied the gall upon the sapling shortly before the escape of the fly. The flies seek by preference the tenderest axillary buds which they begin to prick. When they have selected a suitable bud they poise themselves on its summit and bore the ovipositor obliquely from the surface into the centre of the bud. They lay only one egg in each bud, and this invariably occupies from twenty to thirty minutes. While ovipositing the flies are so indifferent to interruption, that it is possible to cut off the twig which they are piercing, and place it under the microscope for better observation. As soon as one egg is laid they immediately seek out a new bud. The average duration of life in this species is about eight days.

In my experiments in June, 1878, I marked in all twenty-six buds as having been pricked, sixteen indoors

and ten out. By the beginning of July, it was possible to perceive a change in some of these buds, for they were noticeably thicker and larger; and by July 10, I was able distinctly to recognize that it was the *Aphilotrix fecundatrix* gall that was forming. The little oak trees pierced indoors produced three, and those out of doors four galls. It was in this case again remarkable how few of the pricked buds produced galls.

[The hairy catkin gall is found in May on *Quercus sessiliflora*.]

11. Aphilotrix callidoma. Htg.[1]

Gall. These, which are the most elegant of our North German galls, possess a certain historical interest, for they were described by Malpighi[2] in 1682. In spite of this it has only been in quite recent times that its fly has been successfully reared. So far as I know, Giraud[3], in 1859, was the first to breed and describe the fly.

The gall, which springs by a slender stalk of varying length from the axil of a leaf, is spindle-shaped or fusiform, and is marked by regular, sharply defined, longitudinal ribs. It is usually green with ribs of a red colour. (Fig. 11.)

The galls appear at different times, sometimes in July, and sometimes in August. They mature quickly, and the earliest fall to the ground at the end of July. To rear the flies, the mature galls should be collected

[[1] *Cynips callidoma*, Thoms. *Andricus cirratus*, agamous form, Cameron. *Andricus callidoma*, Mayr.]

[2] Malpighi, *Plant. anatom.* II. De gallis.

[3] Signalements, &c. de Cynipides, Verhdl. zool.-bot. Ges. Wien, ix. pp. 337–74.

and left on damp sand until they begin to get brown, which is a sign that the larva is full grown ; they should then be kept in a cool place or in the open air through the winter. Some of the flies appear during the next spring, but others lie dormant until the second year. It is probable that galls maturing early hatch out in the first year, and that those maturing late do so in the second year. It is particularly to be remarked that the majority of the galls are beset with parasites, and this is probably the reason why the fly has not been identified before.

Fly. 4 mm. long ; reddish yellow ; antennae, sutures of the thorax, and margins of scutellum, black ; the back of the abdomen dark brown ; head and thorax sparsely haired ; legs yellowish brown, trochanters only black ; posterior tibiae brown.

Experimental breeding. The flies emerge in April and seek the male catkin buds in which to lay their eggs. For this reason I have only been able to watch them ovipositing in the open air, or on branches cut off for the purpose. The fly lays its egg upon and between the anthers, while they are enclosed in the bud ; and there are often a great many laid in the same bud. In April, 1878, I marked a number of buds pricked in the open air. At the time when most buds were more or less developed those which had been pricked were remarkably backward, only a few flowering catkins projecting from them. On further examination it was seen that the anthers were quite distorted by small closely set galls. This gall, which I am about to describe, was that of *Andricus cirratus.*

[The stalked spindle gall is found in July and August on *Quercus sessiliflora*.

Inquilines. *Synergus nervosus* and *S. vulgaris*.

Parasite. *Siphonura brevicauda*. Cameron considers *Aphilotrix callidoma* the same as *Aphilotrix quadrilineata* and says he can find no distinguishing characters in the two flies. Cameron, *Hymenoptera*, vol. iv. p. 97.]

11a. Andricus cirratus. n. sp.

This gall has not been described before. I have chosen the title *cirratus* on account of the tuft of hair (*cirrus*) which the gall bears on its apex.

Gall. Size about 2 mm.; oval with a rounded point; when fresh of a green, and when mature of a brownish colour. The rounded end of the gall bears a tuft of long thick whitish hairs three or four times the length of the gall. The gall is placed on the stalk of the male catkin; at its base two shallow impressions may be recognized which are derived from the sutures of the anthers from which the gall sprang. The galls are often placed so closely together that they appear to form one woolly mass; the separate catkins are then more or less distorted and only a white tuft of hair can be seen projecting from the open bud. (Fig. 11 a.) The fly is very easily reared if the galls are collected at the end of May or the beginning of June.

Fly. Length 1·5 mm.; black; thorax dull; scutellum rough; abdomen reddish yellow on the sides; legs uniformly citron yellow, the posterior trochanters dark; antennae testaceous with dark apices. The males are similarly coloured, but the abdomen is somewhat lighter.

Experimental breeding. When in the beginning of

June, 1878, a great number of the flies had emerged, I put them, on June 8, on an oak sapling and saw them begin to prick the small axillary buds, of which fourteen in all were marked. About four weeks afterwards, on July 5, I observed galls developing on three buds, which, as they grew out of the buds with long stalks, were soon recognizable as *Aphilotrix callidoma* galls. In the beginning of August two more galls developed; the cause of this delay is difficult to explain, as all the buds were certainly pricked at the same time. The gall grows very quickly, reaches maturity in three weeks, and then falls to the ground.

[The tufted gall is found in May on *Quercus sessiliflora.*]

12. Aphilotrix Malpighii. n. sp.[1]

Gall. This gall is very like the preceding one and of the same spindle shape, but shorter and more compressed; and it is usually either without a stem or with a very short one. The time of maturity is different: it appears much later than the former gall, does not show itself out of the bud until September, and arrives at maturity in October. (Fig. 12.)

The development of this fly differs from the preceding. The gall which matures in October undoubtedly contains the full grown larva, but this does not enter the pupa state in the same year. It rests till the next year,

[1] On account of the great resemblance to the *Aphilotrix callidoma* gall it has often been confounded with it, but the fact that it possesses a totally different sexual generation marks it as a separate species. In memory of the circumstance that Malpighi nearly 200 years ago described the *Aphilotrix callidoma* gall, I have called the present species after him. [*Andricus Malpighii*, Mayr.]

enters the pupa state in the autumn, and the flies emerge in April of the second year.

Fly. 3 mm. in length; reddish yellow, darker than *Aphilotrix callidoma*; thorax with black streaks, upper part smooth, sides sparsely haired, scutellum rough; back of the abdomen dark brown; legs reddish yellow, trochanters all brownish, as well as the upper half of the femora and outer surface of the tibiae; antennae black. The colouring of this fly is so like that of *Aphilotrix callidoma* that it can only be distinguished with certainty from it when it has been reared from the gall. I have not been able to make experiments in breeding with this fly, but I have made some experiments with the corresponding sexual generation and these have afforded me trustworthy results.

[Malpighi's gall is found in September on *Quercus sessiliflora*.]

12[a]. Andricus nudus. n. sp.[1]

Gall. This little inconspicuous gall, 1·5 mm. long, of an elongated oval form, with distinctly depressed apex, is found on the flower stalks of the male catkins between the anthers. The gall is naked but at its point it has a few little hairs. When fresh it is green but yellow when mature. (Fig. 12[a].)

To rear the flies the galls must be collected at the end of May; the flies emerge in June.

Experimental breeding. I succeeded in breeding these flies without any difficulty. In 1877 I made my first experiment. A quantity of fecundated females

[1] This species also has hitherto been undescribed. I have chosen the name *nudus* because it differs from the *cirratus* in being perfectly bald.

were placed upon an oak sapling, and on June 11 ten buds were pricked by them. These active little flies always choose the most tender axillary buds. Care must be taken therefore in experimental breeding to select only those oaks which have buds of a soft and tender consistence. It was long before any change could be seen in the pricked buds, and it was not till September 3 that two of them showed the beginning of gall formation. On October 2 a third gall appeared, and all three galls were those described above as *Aphilotrix Malpighii*. In April, 1879, I got two flies out of these three galls. I made in 1878 a second experiment in breeding with *Andricus nudus*, and from the collected galls I obtained the first flies on May 30. On June 1 I put them on a small oak. I observed that several of them began at once to prick, and eighteen buds were marked in all. In the beginning of September three galls grew out of these buds, and four more at the end of the month; consequently the connexion between *Aphilotrix Malpighii* and *Andricus nudus* appeared to me sufficiently proved.

[The bald seed gall is found on *Quercus sessiliflora* in May.

Fly. Length 1·2 to 1·6 mm. black, abdomen paler, testaceous on ventral surface, thorax slightly shining, legs uniformly yellow; antennae of same colour except the fourth and fifth joints which are darker. Males have the femora and tibiae dark, as also the antennae, except the second and third joints which are bright yellow, mesonotum finely shagreened and shining.]

13. Aphilotrix autumnalis. Htg.[1]

Gall. This gall, like the *Aphilotrix globuli* galls,

[[1] *Cynips autumnalis*, Hartig. *Andricus autumnalis*, Mayr. *Andricus ramuli*, agamous form, Cameron.]

described above, developes from a bud, and its base is surrounded by the bud-scales. It is of an elongated oval shape with a distinctly depressed umbilicus at the apex, and when fresh it is covered with a brown sappy rind. The gall is formed in October, and at the end of the month, when mature, it falls out of the bud to the ground. The sappy rind is then loosened from the woody inner gall, which shows on its surface faintly marked furrows. (Fig. 13.)

The fly does not appear until the second year. The flies emerged in April, 1878, from the galls collected in October, 1876.

Fly. Size 3 mm. long; head and thorax black; the latter dull and wrinkled; abdomen shining, dark on the back, reddish brown on the sides; legs reddish brown, trochanters dark. Appears in April.

It was to be expected that an alternate generation of this species would be found, not only from its great resemblance to *Aphilotrix globuli*, but also from the time of the gall's appearance. The flies emerge in April, but, as the galls are not formed until October, in a winter bud that is not in existence in April, it is evident that another generation, which forms the gall, must intervene. I have not made direct experiments in breeding with *Aphilotrix autumnalis*, but I have watched these flies ovipositing. At first I believed that they would prick flower buds only, as it was these that they pricked so vigorously under my own observation when I put some flies on detached twigs. I convinced myself afterwards that they pricked other buds without making any distinction. Perhaps the flower buds may

receive a preference because they are larger and develop earlier. This fly lays a multitude of eggs in the same bud, and sometimes bores round the whole periphery of the bud, so that later a large number of eggs are found within, each separate, but all packed closely together. The eggs are laid either on the leaves or on the anthers. I have not reared flies from the resulting gall myself, but have ascertained that they belong to the sexual generation of *Aphilotrix autumnalis*, that is *Andricus ramuli.*

[The autumn gall is found in October on *Quercus sessiliflora* and *Q. pubescens.*

Inquilines. *Synergus nervosus*, *S. variolosus*, *S. ruficornis*, and *S. apicalis.*

Parasite. *Megastigmus dorsalis.*]

13a. Andricus ramuli. L.[1]

Gall. This gall, which very frequently developes from the male flower-buds but occasionally from the leaf-buds, resembles a ball of cotton-wool and varies in size, the size depending on the number of single galls in the conglomeration. On transverse section we find an aggregation of small oval galls 2 mm. long, each of which bears a very long tuft of pale yellow hair. These hairs are interwoven so as to resemble a thick white felt and this gives the gall a very dainty appearance. (Fig. 13a.)

The fly emerges in the first half of July.

Fly. 2 mm. long; entirely yellow, with the sutures of the thorax somewhat darker; in the female the back of the abdomen is brown, in the male black; the antennae and legs are uniformly yellow.

[[1] *Teras amentorum*, Htg. *Cynips quercus-ramuli*, L.]

Experimental breeding. As *Andricus ramuli* galls occur here very seldom I have only once been able to make observations on the propagation of the flies. On July 9, 1878, I found several of these flies pricking axillary buds. I marked six of such buds with threads and from two of them in the beginning of October galls of *Aphilotrix autumnalis* developed.

[The woolly or cotton gall is found in May and June on *Quercus pedunculata*, *Q. sessiliflora*, and *Q. pubescens*.

Inquilines. *Synergus facialis*, *S. radiatus*, *Ceroptres arator*, and *Dictyopteryx Loeflingiana*.

Parasites. *Olinx gallarum* in June, *O. debilis*, *Torymus auratus*, *Decatoma Neesi*, *Eurytoma semirufa*, *Pteromalus Ratzeburgi*, *Anthomyia* (*Homalomyia*) *canicularis*.]

III. Dryophanta Group [1].

14. Dryophanta scutellaris. Htg.[2]

Gall. This gall is globular and is always found on the under surface of the leaf. It varies greatly in size and may attain to 2 cm. in diameter. The gall always springs from the veins of the leaf and more frequently from the midrib than from the lateral veins; but it is only connected with the vein by one point, so that on looking down upon the upper surface of the leaf its presence cannot be recognized. The gall is of a white or yellow colour, the side exposed to the sun being of a beautiful red. It appears in the beginning of July, and matures in October. (Fig. 14.)

The fly is easy to rear from the gall, but reports as to the time when it emerges differ. According to some

[[1] *Dryophanta*, Foerster. *Liodora*, Foerster.

[2] *Cynips Quercusfolii*, Lin. *Diplolepis scutellaris*, Oliv. *Cynips folii*, Hartig. *Cynips scutellaris*, Schenck.]

observers the flies appear in October, and according to others not until March. To ascertain the natural time of emergence the galls must be kept in the open air; if they are kept in a room undoubtedly the flies appear in November, but this is not the case if they are kept in the open air. The fly certainly begins in October or November to gnaw a passage from the central chamber in which it lies, towards the periphery, but it does so without quitting the gall. On the contrary the fly allows a thin lamella of the outer rind to remain, but so thin is this layer that the lumen of the passage can be seen through it. Yet weeks may still pass before the fly breaks through this slight barrier and emerges from the gall; this depends entirely upon the weather. If, for example, in December there should be a hard frost, the fly remains within the frozen gall, but as soon as a thaw comes it releases itself, probably because in thawing the gall quickly perishes. I have repeatedly noticed that the warmer days and thaws of January entice the flies out; but when the frost lasts through January the flight of the flies is delayed until February, or even later should the frost continue. In this case many flies do not appear until March.

Fly. Size 4 mm. long; black; vertex of head reddish brown, as also are the sides of the thorax and sometimes the scutellum; abdomen jet black and very shining; legs black except the lower half of the femora and the upper parts of the tibiae which are reddish brown; the wings are long and the whole insect very hairy, the long hairs standing out from the legs and antennae are characteristic; the antennae have thirteen joints.

Experimental breeding. In the year 1876 I made experiments with this fly which showed me that it pricked by preference the little adventitious buds on the trunks of the older oak trees. My first attempts were only made with a few flies in the open air, and the results I then obtained proved later to be incorrect. I repeated the experiments on a larger scale in 1878. I had kept a large quantity of galls out of doors through the winter, and in January the flies began to take flight. I put them on a little oak indoors and observed that after a few days they began to oviposit, choosing the little adventitious buds that were on the stem. The buds were pricked in the following manner. The fly reared itself, directing its ovipositor to the point of the bud, and bored down into it perpendicularly. The fly is armed for this purpose with a tolerably straight and strong ovipositor. Some time is required to complete the act of ovipositing and the fly usually spends half an hour in the pricking posture. In each bud, only one egg is laid. If a pricked bud is examined it will be seen that the egg lies at the base of the bud-axis, in the cambium layer which is continued into the bud, therefore it may be predicted with certainty that a bud-gall will be the result. In my experiments thirty-four buds were pricked between January 20 and January 26, but it was not until the end of April that I was able to observe the beginning of gall formation in any of the buds. The points of the buds became dark blue and soon the dainty velvety galls of *Spathegaster Taschenbergi* became evident; by the beginning of May eleven galls developed on the tree. In the year 1879

I repeated the experiments and again obtained *Spathegaster Taschenbergi* galls.

[The cherry gall is found in July on *Quercus sessiliflora*, *Q. pedunculata*, and *Q. pubescens*.

Inquilines. *Synergus vulgaris*, *S. pallicornis*, in the spring of the second year; *S. Tscheki*, *Sapholytus connatus*, and *Neuroterus parasiticus*.

Parasites. *Syntomaspis lazulina*, May and June of second year; *Torymus abdominalis*, in March of second year, *T. elegans*, *T. incertus*, *T. regius*, and *Callimome antennatus* from March to June of second year. (This last species is sometimes hyperparasitic on the Inquilines.) *Eurytoma nodularis*, *E. setigera*, *E. rosae*. *Megastigmus dorsalis*, *Porizon claviventris*, *Bracon aterrimus* *Orthostigma gallarum*, *Pteromalus fasciculatus*, *P. jucundus*. *Decatoma biguttata*.]

14a. Spathegaster Taschenbergi. Schltdl.[1]

Gall. These dainty little galls measure 2–3 mm. in length; they have a velvety rind with a rounded point of a dark violet colour; this beautiful colour is caused by a peripheral layer of pigment cells, studded over with short white hairs which give the velvety appearance to the surface. The inner kernel of the gall is soft and consists of cells containing starch granules; these are completely eaten up by the larva, so that ultimately nothing is left but a thin rind. (Fig. 14a.) To rear the flies the galls must be collected in the beginning of May and kept in damp sand; the flies appear in the end of May or the beginning of June.

Fly. Size 2–5 mm. long; antennae, head, thorax and abdomen black; thorax smooth and very shining, scutellum dull and not haired; legs yellowish, only trochanters black, wings long and smoked. The male and female similar.

Experimental breeding. Immediately after fecunda-

[[1] *Dryophanta Taschenbergi*, Mayr.]

tion the females begin to lay their eggs. In May, 1878, I experimented with the oak, on which the *Spathegaster Taschenbergi* galls had been formed. The first flies appeared on May 26. Before a fly begins to prick, it may be seen busily engaged in feeling the veins of the leaf with its antennae, and having done so it pierces them, so that the eggs lie in the veins of the leaf. It is essential if the experiments are to succeed that the leaves should be very soft and tender, for full grown leaves do not seem to suit the fly. Only five leaves were pricked in my experiments because some were already too far developed.

In the beginning of July I noticed the commencement of gall formation as a small round gall growing from the midrib of a leaf. Others soon followed, and I obtained in all eight galls which proved to be those of *Dryophanta scutellaris.*

The connexion of *Dryophanta scutellaris* with *Spathegaster Taschenbergi* was thus proved. The statement made in my first communication that *Trigonaspis crustalis* was the sexual generation belonging to *Dryophanta scutellaris* was due to a mistake, which arose from my having made my experiments in the open air where I was not sufficiently able to control them.

[The purple velvet bud gall is found in April on the dormant buds of *Quercus sessiliflora.*]

15. Dryophanta longiventris. Htg.[1]

Gall. This gall like the former one grows from the midrib on the under side of the oak leaves, but is smaller,

[1 *Cynips longiventris,* Htg.]

being at most 1 cm. in diameter. It is brilliantly coloured, prettily striped with white and red, and the outer rind is smooth or somewhat nodulated. (Fig. 15.)

Rearing the fly is simple if the galls are collected in October when they mature. I have obtained the flies at the end of November and in December. Although the gall is not scarce, it is difficult to obtain any large number of flies, as most of the galls are infested with parasites.

Fly. 3–4 mm. long; black; the margin of the orbits, sides of the thorax, two stripes on the meso-thorax, and the scutellum are reddish brown; abdomen black and very shining; legs reddish brown, trochanters and upper halves of the femora black; the pubescence is the same as in *Dryophanta scutellaris*, from which it cannot in other respects be distinguished with certainty.

Experimental breeding. On account of the small number of these flies procurable, I had great difficulty in getting any results from experiments. In November, 1877, I put several flies on a little oak and observed that, like *Dryophanta scutellaris*, they sought out the younger adventitious buds and pierced them. It was therefore probable that a similar bud-gall would be formed, but the result was negative, for I obtained no gall. My second experiment, made in 1878, was also negative. For the third time, I tried to secure a gall in November, 1879; several buds were pricked and I succeeded in April, 1880, in obtaining two galls. They were very like those of *Spathegaster Taschenbergi*, but with care it was not difficult to distinguish between the two. This result was the more interesting because it was now clear to me that I had hitherto mixed up

this undescribed species with *Spathegaster Taschenbergi.* In 1876 (when I did not know the connexion that existed between the last two species) I obtained, from an experiment I then made, galls of *Dryophanta longiventris* upon leaves which I believed had only been pricked by *Spathegaster Taschenbergi.* Among the collected *Spathegaster Taschenbergi* galls I ought to have observed that there were some of which the colouring was different; these resembled the galls which I now obtained from my experimental breeding with *Dryophanta longiventris.* This gall, which I am now about to describe, is that of *Spathegaster similis.*

[The striped gall is found in July on *Quercus pedunculata.* When attacked by inquilines it often remains very small.

Inquilines. *Synergus pallicornis* and *S. apicalis.*

Parasites. *Syntomaspis cyanea, S. lazulina, Torymus abdominalis* and *T. regius, Callimome longiventris, Elachestus cyniphidium.*]

15[a]. Spathegaster similis. n. sp.[1]

Gall. About 2 mm. long; like *Spathegaster Taschenbergi* but more slender and pointed; of greenish grey colour and with a velvety rind. The colour is caused by a peripheral layer of cells containing a greenish pigment, but this tint is rendered dull by a covering of long white hairs, imparting to it a grey tone. It is especially the stronger and longer pubescence which is the important distinction between this and the *Spathegaster Taschenbergi* gall. (Fig. 15[a].)

These galls are found almost exclusively on the adventitious buds at the base of old oaks; but it may

[1] So called on account of its close resemblance to the *Spathegaster Taschenbergi* gall.

happen that they grow out of the buds of last year's shoots, and then they are not unfrequently formed on the trunk of the tree.

That the two species of *Dryophanta* just described should both seek the little adventitious buds at the foot of the oak, is probably due to the fact that these buds are the first to be reached in spring by the rising sap, and therefore they are able to support gall formation while the higher buds are still dormant. It is of advantage to the summer generations of *Dryophanta* that their flies should be enabled to leave the galls as early as possible, since by doing so they are the sooner safe from the attacks of parasites. The flies emerge from *Spathegaster similis* galls in May, almost a fortnight earlier than from *Spathegaster Taschenbergi* galls.

Fly. 2 mm. long; black, sufficiently like *Spathegaster Taschenbergi* to be confused with it, and only to be distinguished from it by the darker colouring of the legs; these are dark yellow, the outer margins of the femora and tibiae black.

[The green velvet bud-gall is found on dormant buds of *Quercus pedunculata* in April.]

16. Dryophanta divisa[1].

Gall. Of the size of a buckshot; several are usually found together on the under side of the leaves, springing from the veins of the leaf; at first of a bright red colour but this at maturity passes into a brown. The

[[1] *Cynips divisa*, Hartig.]

gall appears at the end of June and ripens in October. (Fig. 16.)

Fly. The flies are from 4 to 5 mm. long; brownish red, with antennae, sutures of the thorax, two stripes on the mesothorax, and the back of the abdomen black; the legs are brown, the trochanters and tarsal segments partly black; pubescence the same as in *Dryophanta scutellaris.* The fly usually emerges at the end of October or beginning of November and sets to work at once to prick the buds. This is another confirmation of a rule that holds good without exception, that gall-flies begin to lay their eggs immediately after leaving the galls, and that no fly passes the winter outside the gall to lay its eggs in the buds early next Spring. With this fly I have made many experiments.

Experiments in breeding. In October, 1877, I placed several flies on a little oak and covered it over. In the beginning of November I noticed that the flies were pricking the buds. Unlike the two former species of *Dryophanta* they did not choose the little adventitious buds, but selected the large terminal ones. The ovipositor was applied as before to the point of the bud, and bored perpendicularly into it. On examining a pricked bud I found two eggs laid on the rudimentary leaves. I knew therefore that more than one egg was laid in a bud, and I was enabled to predict that the galls would be formed on the leaves. But this prediction was not yet to be confirmed, for I obtained no galls.

In the year 1878, I repeated the experiment; after a number of flies had been enclosed, they began to prick the buds on October 28. The flies remained alive

about fourteen days and pricked a series of buds during this time. After their death I took the oak out of doors for the winter, but next year in the beginning of May, when the buds began to shoot, I brought it indoors again for more convenient observation. When the leaves unfolded, dainty little galls appeared upon them, five in all, besides one which grew directly out of a bud. This gall, produced by *Dryophanta divisa*, is that of *Spathegaster verrucosus*.

[The scarlet pea gall is found in June on *Quercus pedunculata*.

Inquilines. *Synergus pallicornis*, in April of the second year; *S. Tscheki*, in March of the second year; and *S. albipes*, in August of the same year.

Parasites. *Syntomaspis cyanea*, in spring of the second year; *S. lazulina, Torymus abdominalis, T. pubescens. T. regius, Pteromalus Saxesenii, P. fasciculata*, all in autumn of the same year; *P. incrassatus*, in May of second year; *Eurytoma squamea, E. setigera, E. signata, E. rosae, Decatoma biguttata, Eupelmus urozonus.*]

16ª. Spathegaster verrucosus. Schltdl.[1]

Gall. About 4 mm. long; oval in form, with broad rounded point; of a greenish yellow or somewhat reddish colour; with a peculiar granular but rather glossy rind, caused by the peripheral cells bearing, instead of hairs, small round bladders filled with a clear fluid, probably a protection against parasites. The situation of the galls is peculiar because they grow sometimes on the leaves, sometimes on the shoots, and sometimes from the buds; this is due to the fact that although as mentioned above the egg of *Dryophanta divisa* is usually laid on the rudimentary leaves, yet

[[1] *Dryophanta divisa*, sexual form, Cameron. *Dryophanta verrucosa*, Mayr.]

in some cases it may come to lie in other situations. A slight pushing of the egg higher up or deeper down makes all the difference as to the position of the gall. If the egg lies on the point of a leaf, the gall developes on that spot, and the full grown leaf bears a gall on its point; but if the egg lies deeper in the base of the leaf, the whole leaf-surface is absorbed, and the gall rests directly on the shortened petiole. It may appear sometimes as if the gall had sprung from the shoot itself, but in the angle which it forms with the shoot there is always a little axillary bud, a proof that the gall is merely substituted for the leaf. Lastly, when the egg is sunk still deeper into the axis of the bud, the whole bud is absorbed in the gall formation, or in other words a bud-gall is formed. These different varieties are illustrated. (Fig. 16a.)

The gall matures in the end of May and the flies emerge in the last days of May or in the beginning of June.

Fly. Size 3 mm. long; black; thorax smooth and shining, the sides only faintly punctate, the scutellum rough, on the metathorax a scanty white pubescence; abdomen brilliantly jet black; legs orange, trochanters black; males have similar colouring, but darker legs.

No experiments have been made with this fly, but as the formation of the gall by the agamous generation, *Dryophanta divisa*, has been established, there is no doubt that *Spathegaster verrucosus* is the sexual generation belonging to it.

[The red wart gall is found in May on *Quercus sessiliflora*.]

IV. Biorhiza Group [1].

17. Biorhiza aptera. Fbr.[2]

Gall. This gall is formed only on oak roots, and on the smallest as well as on the thickest. When it first bursts through the cortex it is soft and of a pink colour, but at maturity it becomes brown, hard and woody. The galls vary much in size, the smallest being about the size of a pea. They are rarely isolated, and are usually united into a large mass. (Fig. 17.)

Owing to their obscure situation it is not easy to procure the galls, but the flies may be collected when they appear on the oak. The time given by different authorities for their appearance varies, some having found them in November, and some in March; according to my own observations the latter date must be considered as exceptional, at least in this place. I have for many years found the flies regularly in the end of December and beginning of January.

Fly. Size 4–7 mm. long; wingless; thorax slender, pilose at the sides; the whole insect yellowish brown; the abdomen darker, with an almost black transverse band across its middle; legs of same colour; size of the fly very variable.

Experimental breeding. I have made many attempts at breeding with *Biorhiza aptera*, and I was very soon satisfied that the flies do not go to the roots of the oaks to deposit their eggs, but rather try to ascend by

[[1] *Biorhiza*, Westwood. *Apophyllus*, Hartig. *Teras*, Hartig. *Dryoteras*, Foerster.

[2] *Cynips aptera*, Fab.; *Biorhiza terminalis*, agamous form, Cameron.]

creeping up the trunks. They then seek by preference the greater terminal buds, and begin to bore into them. The pricking is done in a very different way from that of other gall-flies. After a suitable bud has been found, the fly stops, turns with its head downwards, and directs its abdomen to the point of the bud. In this position it inserts its ovipositor somewhat below the middle of the bud, and bores straight towards the base. The egg comes to lie deep in the bud, in or upon the tissue from which the terminal growth proceeds. After the fly has pushed in its ovipositor it withdraws it, and goes on boring one canal after another in the stratum which the egg is to occupy, until the whole layer is riddled like a sieve. When the operation is finished, the eggs are successively pushed into the pricked canals, where they lie so thickly together that they look like a continuous mass. The amount of work which the fly goes through in laying its eggs in this way is astonishing. After having been occupied for hours in boring these numerous canals, it appeared to me at first inexplicable that it had as yet laid no eggs; I found, however, that it bores all the canals for their reception before actually laying a single egg. This part of the work requires much time, as to which I have made the following observations.

On January 27, 1878, a fly was put upon a little oak, and soon began to prick a bud; when it had finished the first bud, it went on without interruption to another, and was altogether eighty-seven hours busily employed in laying its eggs. In these two buds I counted 582 eggs.

For actual breeding purposes I allowed the flies to pierce two little oaks ; on these they pricked six buds. In the beginning of May two buds showed evidences of gall formation : at the base of the bud a swelling formed rapidly, and the real bud seemed to be absolutely raised and set loosely on the gall, a proof that gall formation springs from the meristem at its base. At the end of May the galls were fully grown, and proved to be those of *Teras terminalis*[1]. Whether the experiments with *Biorhiza aptera* are made indoors or out, it will always be found that in many of the buds no gall formation occurs : the reason of this being that the ovipositor of the fly causes an extensive destruction of the tissues of the plant, and if no zone at the germinal point remains intact, gall formation cannot take place. The development of the bud is impossible where the whole bud-axis is cut through.

17a. **Teras terminalis.** Fbr.[2]

Gall. This gall grows, as the name indicates, chiefly from terminal buds, but sometimes it may be found

[1] The connexion of the two generations *Biorhiza aptera* and *Teras terminalis* has also been proved by Dr. M. W. Beyerinck, as I see in a communication to the *Entomologische Nachrichten*, vol. vi. p. 45 (March, 1880). See Beyerinck, *Bijdrage tol de Morphologie der Plantegallen*, Utrecht, 1877.

[The root gall is found in September and October on *Quercus pedunculata*, *Q. sessiliflora*, and *Q. pubescens*. The gall lives about fourteen months.

Parasite. *Torymus nobilis*. It is stated by Curtis and others, that *Biorhiza aptera* is polyphagus and occurs on beech roots. Cameron, *Hymenoptera*, vol. iv. p. 13.

[2] *Cynips quercûs-terminalis*, Fbr.]

springing from an axillary one. It is spherical, varying in diameter from 1–4 cm. When fresh it is of a pale colour often beautifully tinted with rose, resembling an apple. At first its tissue is soft and sappy, but at maturity it becomes hard and woody within, while its periphery changes to a loose spongy mass; in the woody kernel lie countless larva chambers. (Fig. 17 a.) The gall matures in June, and the flies emerge in July. Owing to the great abundance of the gall, the flies can be reared in large quantities without difficulty, although the galls are much interfered with by parasites, particularly by the larva of one of the *Curculionidae*, *Balaninus villosus*. I have frequently found this rather rare beetle in the gall of the *Teras terminalis*. It hollows out a perpendicular channel with its long thin proboscis, lays an egg, and pushes it down into the end of the passage. Afterwards, when the larva escapes from the egg, it eats its way through the gall in various directions; as it happens that several eggs are usually laid in a gall, the gall is so completely wormed through by the grubs, that often not a single larva chamber remains undisturbed.

Fly. Size 3 mm. long; of a uniform yellow colour; abdomen darker, especially on the dorsum; the males are paler in colour, and are winged; the females are wingless or with rudimentary wings only.

Experimental breeding. I made my first experiments in July, 1876. I put a large number of flies on one of the little oaks under a covering, and observed them for several days indoors. When the flies began to lay their eggs, I was at first surprised to find that they

pierced not only the bark of the roots, but also the buds and even the leaf-stalks. To be perfectly sure, I examined the pricked buds and leaf-stalks, and found unmistakable bored canals with the eggs in them. When the time of gall formation arrived, towards the end of August, I observed bright red galls growing out of one leaf stalk, several buds, and some spots in the bark of the root. They grew slowly; by the end of September some of the root-galls were from ·5 to 1 cm. in diameter, but the bud and leaf-stalk galls were only the size of a pea. In October these lost their brilliant red colour, and dried up. The root-galls appeared at first to pass the winter well, but finally perished, and I did not succeed in obtaining a single fly.

In July, 1878, I repeated the experiments, and I obtained some bud-galls, and also some root-galls which I brought to full development. In October the growth of the galls ceased; they were of soft, sappy consistence, and the larvae were very small, but next spring they came to their full growth, and began to get woody. By an unlucky chance I obtained no flies from these galls. This experiment was interesting, as it confirmed my previous observation that *Teras terminalis* pricks buds. To consider this as a mistaken instinct, appears to me erroneous; I rather incline to the view that in the phenomenon we have a peculiarity transmitted from the apterous generation. The two generations are so remarkably alike, that with the exception of the presence of male flies in *Teras terminalis* no distinction can be found, the female flies being exactly similar; and their close relationship is still further

shown by the fact that in *Teras terminalis* some flies preserve the habit of pricking buds like their mother flies. Here the great resemblance of the two flies, in spite of their different development and manner of life, is striking [1]. Since *Biorhiza aptera* is wingless, it need cause no surprise that the *Teras terminalis* generation is also deficient in wings, for we must remember that although the males are always provided with perfect wings, yet the females are either wingless or have short rudimentary wings only. Are these rudiments to be considered as organs in the process of development or of degeneration? I believe that the decision must depend on whether the possession of perfect wings would be more advantageous than the present rudimentary ones. It must be apparent to anyone who watches the flies while pricking, that perfect wings could be of no great use to them. The fly does not need wings to reach the place where it is to lay its egg, as it has only to creep down the trunk to get at the roots; but having done this it has in addition to penetrate the ground, which it accomplishes by pushing its way backwards with the aid of its abdomen. In the act of burrowing, wings could only be a hindrance, therefore the apterous condition is a decided advantage to the fly.

There is a curious phenomenon in the propagation of *Teras terminalis* which deserves notice. It appears that while some galls produce both sexes, some yield only

[[1] Another point of resemblance is found in both generations possessing a disagreeable bug-like smell, which is probably defensive in character, as it persists after ovipositing is over.]

females, others only males. It seems probable also that some specimens of *Biorhiza aptera* produce only males and some only females. We are therefore driven to admit that the sexes are differentiated in the egg, and that this phenomenon cannot be referred to any other influence, such as different or more abundant nourishment of the larvae.

[The oak apple is found in May on *Quercus pedunculata*, *Q. sessiliflora*, and *Q. pubescens*. According to Mayr, the gall-makers, as well as the inquilines and some parasites, make their appearance in the end of May or the beginning of June. In June the Rosechafers (*Cetonia*) eat their way into these galls, consuming the outer spongy tissue, and leaving the inner cells adherent to each other. From these inner cells parasites are produced in the second year. A large caterpillar, probably of a Noctua, sometimes consumes the whole interior of the oak apple.

Mr. Francis Walker gives the following list of insects inhabiting oak apples:—

June (1845). *Nitidula grisea*. *Balaninus glandium*, *Forficula auricularia*, *Psocus subocellatus*, *Atropos* ——?, *Synergus socialis*, and specimens of two or three other species of *Cynipidae*, *Pteromalus Naubolus*, *Pteromalus* ——?, *Pteromalus semifascia*, *Pteromalus ovatus*, *Pteromalus domesticus*, *Eupelmus urozonus*, *Eulophus gallarum*, *Cecidomyia* 2 sp., *Tortrix viridana*.

July. *Physoevria* ——?, *Nitidula grisea*, *Latridius lardarius*, *Corticaria transversalis*, *Carpalimus fuliginosus*, *Aleochara* ——?, *Orchestes quercus*, *Pimpla* 2 sp., *Hemiteles areator*, *Synergus socialis*, *Decatoma immaculata*, *Megastigmus dorsalis*. *Callimome cingulatus*, *viridissimus*, *parellinus*, *inconstans*, *confinis*, *minutus*, *exilis*, *chlorinus*, *mutabilis*, *latus*, *leucopterus*, *abdominalis*, *leptocerus*, *autumnalis*. *Pteromalus Naubolus*, *dilectus*, *fuscipennis*, *fasciiventris*, *ovatus*, *hilaris*. *Eupelmus urozonus*. *Tetrastichus diaphantes*. *Eulophus gallarum*, *Agathyllus* ? sp. *Inostemma Boscii*. *Ceraphron* ——?. *Drosophila* ——?. *Lozotaenia xylosteana*, *Zeiraphera communana*. *Chaetochilus sylvellus*. *Pentatoma lurida*. *Anthocoris nemorum*. A few *Arachnidae* and *Acari* of such species as dwell under the bark of trees.

August. *Dromius quadrimaculatus*. *Cryptophagus cellaris*. *Corticaria transversalis*. *Microgaster* ——?. *Aphidius* ——?. *Synergus socialis*. *Decatoma immaculata*. *Megastigmus dorsalis*. *Callimome*,

same species as in July. *Eupelmus urozonus. Tetrastichus diaphantes. Chaetochilus sylvellus. Aphis* —— ?. *Thrips* —— ?. *Pteromalus Naubolus, dilectus, fuscipennis, platynotus, planus, dubius, fasciiventris, decidens, ovatus.*

September. *Cryptophagus cellaris. Latridius transversus, Corticaria transversalis. Megastigmus dorsalis, Callimome,* same species as in July. *Pteromalus Naubolus, dilectus, decidens, ovatus,* and two doubtful species. *Eupelmus urozonus. Ceraphron,* two doubtful species.

October. *Megastigmus dorsalis. Pteromalus dilectus, ovatus. Tetrastichus diaphantes.*

December. *Megastigmus dorsalis. Callimome nigricornis.*

January (1846). Same.

February. Same, and *Pteromalus domesticus. Eulophus gallarum.*

March. *Bracon* —— ?. *Synergus socialis. Callimome nigricornis. Pteromalus domesticus. Eulophus gallarum.*

April. *Synergus socialis, S. facialis. Megastigmus dorsalis. Callimome nigricornis. Pteromalus Naubolus. Eulophus gallarum.*

May. Same, and *Pteromalus ovatus.*

June. *Megastigmus dorsalis. Pteromalus Naubolus, ovatus. Eupelmus urozonus. Tetrastichus diaphantes.*

From a number of *Teras terminalis* galls, Mr. Walker collected more than 55,000 specimens belonging to 75 species distributed as follows. *Coleoptera* 9 species, 191 specimens; *Orthoptera* 1 sp., 5 specimens; *Neuroptera* 2 sp., some hundreds of specimens; *Hymenoptera* (*Cynipidae*) 4 or 5 species, 30,246 specimens; *Hymenoptera* (parasitic) 45 sp., 24,417 specimens; *Diptera* 3 sp., 23 specimens; *Lepidoptera* 5 sp., 9 specimens; *Hemiptera* 5 sp., 51 specimens; *Arachnidae* and *Acari* 5 or 6 sp.

All the *Coleoptera, Orthoptera, Neuroptera, Diptera, Lepidoptera, Hemiptera,* and *Aptera,* with the exception of *Balaninus glandium* and *Drosophila,* were probably accidental visitors.

See Walker, *Zoologist,* iv. pp. 1454-57 (1846); *Entomologist,* v. p. 432 (1871), and ix. p. 29 (1876).

Mr. Cameron has only met with one inquiline, *S. facialis,* and gives the following list of parasites bred from *Teras terminalis*:—

Torymus abdominalis = cingulatus = cyniphidum. T. regius = inconstans. T. longicaudis = leucopterus. T. auratus = viridissimus = autumnalis = confinis = mutabilis = leptocerus = minutus = muscarum = propinquus = nanus = appropinquans = gallarum.

Syntomaspis caudata = crinicaudis.

Megastigmus dorsalis = Bohemanni = xanthopygus.

Eurytoma rosae.
Decatoma biguttata, D. immaculata, D. signata.
Eupelmus urozonus.
Olinx scianeurus = euedoreschus.
Eulophus gallarum, E. agathyllus, E. ramicornis.
Tetrastichus diaphantes.
Pteromalus (Walker's list), *P. cordairii, P. meconotus, P. stenonotus. P. leucopezus, P. gallicus, P. Dufourii.*
Platymesopus Westwoodi, P. Erichsoni.
Dendrocerus Lichtensteinii.
Inostemma Boscii.
The following probably hyperparasitic:—
Pimpla calobata, P. caudata, P. alternans.
Hemiteles areator, H. coactus, H. punctatus.
Lampronota segmentata.
Cryptus hortulanus.
Bracon caudatus.
Apanteles breviventris.
Microtypus Wesmaelii.
Microdus rufipes.
Ratzeburg gives also:—
Entedon amethystinus, E. deplanatus, Geniocerus cyniphidium, Eupelmus azureus, Mesopolobus fasciiventris, Torymus admirabilis, T. incertus.]

18. Biorhiza renum. Htg.[1]

Gall. These little kidney-shaped galls, generally found in great numbers on the under side of the leaves, are arranged in rows attached to the veins. The gall is of a green or yellowish colour sometimes tinted with red. It is formed in September, attains maturity in October, and then falls to the ground. (Fig. 18.)

Notwithstanding the enormous abundance of the galls, attempts at rearing do not always succeed. When the galls fall in October, the larva has not attained its full growth, and they must therefore be kept on damp sand.

[[1] *Trigonaspis megaptera*, agamous form, Cameron. *Trigonaspis renum*, Mayr.]

When they have acquired by degrees a dark brown colour, we may consider that larval growth within them is complete, but the galls must still be left the whole winter in the open air. The larva then passes the following year as such, and in October assumes the pupa state. The flies appear in December and January, but there is always a fair proportion of galls from which insects do not emerge until the third year.

Fly. Size 1·5 mm.; wingless; the whole fly brownish red; legs light yellowish brown; thorax dull and punctured; scutellum hairy; abdomen almost sessile and very shining, vertex finely shagreened, in the middle line a shallow furrow with a little protuberance on each side. Antennae of thirteen joints, labial palpi of two joints, maxillary palpi of four joints.

Experimental breeding. I could not at first discover where this species laid its eggs. It was very certain that the insect which emerges in January could not be the author of the galls of *Biorhiza renum* formed on the leaves in September. A consideration of the structure of the ovipositor would lead one to imagine that the insect punctures buds, but I could not at first succeed in seeing the fly lay its eggs. In December, 1878, I reared a certain number of flies which I placed upon a little oak. At first they remained perfectly still, then they began to move about, and feel the adventitious buds on the stem with their antennae. At last they pierced a few of the buds, and at the end of April in the following year a little red gall, which I soon recognized as that of *Trigonaspis crustalis*, grew from two of these buds.

[The kidney gall is found in September. This gall grows only in the shade, and on the north side of trees of *Quercus pedunculata*, *Q. sessiliflora*, and *Q. pubescens*.

Inquilines. *Synergus varius*, *S. vulgaris*, *S. tibialis*, *S. ruficornis*, *S. pallicornis*, and *S. Thaumacera*, in April of second year.

Parasites. *Callimome fuscicrus*, *Mesopolobus fasciiventris*, *Pteromalus Saxesenii*, *Pleurotropis cyniphidium*, *Anthomyia gallarum*.]

18a. Trigonaspis crustalis. Htg.[1]

Gall. These round, sappy, red and white galls vary in size from that of a pea to a cherry. They are found most frequently low down on the trunks of old oaks, often crowded together, but they also occur on small last-year shoots. The gall always grows out of a bud, and it is therefore not a bark gall. On old oaks it is often found quite hidden under moss, so that it certainly appears then to grow directly out of the bark, but this is not the case. If the base of the gall be examined, it will be found invariably to originate in a bud. (Fig. 18a.)

To rear the Fly, it is necessary that the galls, which are very succulent, should be gathered at the end of May, shortly before maturity. Most of the flies emerge from the beginning to the middle of June.

Fly. Size 4 mm. long; head and thorax black; abdomen bright orange, blackish at the apex only, shining, distinctly pedunculate, and of a rounded form; legs orange; wings very long; males and females similar in colouring; antennae of the male 15-jointed, of the female 14-jointed; labial palpi 3-jointed, maxillary palpi 5-jointed.

Experimental breeding. I had repeatedly watched

[[1] *Cynips megaptera*, Pz. *Trigonaspis crustalis*, Htg. *T. megaptera*, Mayr. *Cynips crustalis*, Thoms.]

this fly ovipositing in the open air before I succeeded in being quite certain what gall it produced. From the structure of the ovipositor resembling that of *Spathegaster Taschenbergi*, I suspected that it too pricked leaves. At length I observed in June, 1876, several flies pricking the veins on the under sides of oak leaves: I was deceived by an unfortunate accident, and led to assert that *Trigonaspis crustalis* produced *Dryophanta scutellaris* galls, which also occur on leaves[1]. In the year 1878, I made a successful experiment in breeding on isolated oaks with *Trigonaspis crustalis*. It is not difficult to make the flies oviposit provided we have an oak with quite tender leaves at our disposal. The flies do not touch full-grown leaves, they only select those with veins still soft and tender. They usually prick the leaves in the evening, or in deep shade in daytime. The fecundation of the females must first take place.

If the fly is going to oviposit, it can be recognized at once by the characteristic position it assumes; first it wanders over the under surface of the leaves, incessantly using its antennae, at last it stops, directs its abdomen almost perpendicularly towards the angle formed by the vein of the leaf with the leaf-surface, and then cuts into the side of the vein. *Trigonaspis crustalis* makes a whole row of punctures into a single leaf, and the wounds in the veins can be plainly distinguished after-

[1] On June 24, 1876, several leaves were pricked under my eye by *Trigonaspis crustalis*. In July, *Dryophanta scutellaris* galls were formed upon them. These same leaves had also been pricked by *Spathegaster Taschenbergi*, and as I had omitted to examine them again later, I did not know that other galls were forming there.

wards. I allowed the flies from June 6 to 12 to prick indifferently two little oaks, one of which I then kept indoors, and the other out. The next two months passed without any trace of gall formation being discernible. At the end of August I examined some of the leaves, and found eggs in the scars of the punctures which were still visible; these contained living and moving embryos. At last, on September 6, there appeared simultaneously out of several leaf-veins little whitish galls which grew very slowly, and three weeks more elapsed before they could be positively recognized as those of *Biorhiza renum.* On one oak sixty, and on the other about seventy galls were formed. The observation of the generation-cycle was thus complete.

On account of the morphological features of interest which these two generations offer, I have given a drawing of both flies. (Fig. 18–18[a].)

A comparison of the two generations shows some very striking differences: the form, size, and colouring are utterly unlike, and the variation extends to other parts of the body. In *Trigonaspis crustalis* the antennae are respectively 14 and 15-jointed, the maxillary palpi 5-jointed, and the labial palpi 3-jointed. On the other hand, in *Biorhiza renum* the antennae are 13-jointed, the maxillary palpi 4-jointed and the labial palpi 2-jointed. Lastly the ovipositor is of a totally different construction (see illustration, Pl. III. 6, 6[a]). Owing to these and other important differences, the two generations would undoubtedly have been considered as belonging to different genera.

[The pink wax gall is found in May on dormant buds of *Quercus sessiliflora* and *Q. pubescens.*

Inquilines. *Synergus thaumacera* in June and July of same year; *Synergus facialis*, *S. erythrocerus*, and *S. pallicornis.*

Parasites. *Torymus amoenus*, *T. flavipes*, *Syntomaspis fastuosa*, *Callimome rubriceps*, and *Limneria exareolata.* Birds frequently pick the larvae out of these galls.]

19. Neuroterus ostreus. Htg.[1]

Although I have not succeeded in fixing the generation-cycle of this fly, it appears to me desirable to include a notice of this species. Until now it has been classed with *Neuroterus*, but it differs so materially from the species of *Neuroterus* before described that I propose to separate it from them.

Gall. This dainty little gall is spherical; 1–2 mm. in diameter; grows generally from the midrib on the under side of the oak leaves, and is at first enclosed between two brownish scales. Later it grows beyond the scales which then fall off; it is of a pale yellowish colour, very often marked with red spots. The gall appears in August and September, and when mature falls to the ground. (Fig. 19.)

When the gall becomes detached from the leaf, the larva is still small; it is therefore necessary to keep the galls for some time on damp sand. I have had some difficulty in rearing any considerable number of these flies, because as a rule the great bulk of the galls are beset with parasites. Meantime, however, I have ascertained that the flies appear at various times. In galls maturing early, larvae are full grown at the beginning of September, and the flies emerge towards the end of

[[1] *Andricus ostreus*, Mayr.]

October, in the same year. On the other hand, those galls which mature in October do not yield their flies in the same year, but these pass the winter in the pupa state, and appear next March.

Fly. Length 2·5–3 mm.; black; thorax dull, thinly covered with whitish hairs, scutellum rugose; antennae black, pale at the base; legs uniformly orange.

Attempts at breeding with this fly have been made without any results. I succeeded in getting some flies, which were hatched in October, 1878, to prick the buds, but no galls were formed. There can be no doubt, however, judging by the formation of the gall, that a generation alternating with this species does exist. The flies emerging in October and March cannot directly produce the galls which appear in August; and as these galls spring from the midrib of a leaf late in the summer, it is clear that another generation must have laid the egg. I strongly suspect that the sexual generation belonging to *Neuroterus ostreus* is to be sought for in *Spathegaster Aprilinus*[1]. The construction of the ovipositor which is specially designed for boring the ribs of leaves, and a certain general similarity in the flies, bear out this view.

[[1] Professor Mayr informs me that this conjecture has since proved to be correct. Beyerinck, however, describes a sexual generation inhabiting a small bark-gall growing on the bud-ring which he calls *Neuroterus farunculus*, but he gives no details. (*Beob. üb. d. e. Entwick. e. Cynipiden-Gallen*, p. 37, note.) He also states that he bred *Neuroterus Aprilinus* from the galls of *Aphilotrix solitaria* (l. c. p. 138, note); and Schlechtendal and Loew consider that *Neuroterus Schlechtendali* is the agamous form of *S. Aprilinus*. *Neuroterus Schlechtendali* is a small gall, 1 mm. in length, green at first, afterwards brown, springing from a dilated part of the catkin in May on *Quercus pedunculata*, *Q. sessiliflora*, and *Q. pubescens*. It emerges in July of the second year.]

[The oyster gall is found in August on *Quercus sessiliflora*, *Q. pedunculata*, and *Q. pubescens*.

Inquilines. *Synergus tristis* in April, and *S. Tscheki* in June of second year.

Parasites. *Pteromalus bisignatus, Eurytoma rosae, Aulax syncrepidus.*]

19a. Spathegaster Aprilinus. Gir.

Gall. The galls spring from buds and are of different sizes. They are round, of a pale or greenish yellow colour, and are surrounded at the base by bud-scales. They are very thin-walled and each contains one or more larva chambers which may sometimes be recognized through the outer wall. The gall appears in the end of April or beginning of May, and matures very quickly. (Fig. 19a.)

The fly emerges in the end of May.

Fly. Length 2·5 mm.; black; thorax somewhat shining, scutellum wrinkled; abdomen shining; antennae black; legs dark yellow, coxae and basal half of the femora blackish; males and females similar in colouring. I have not succeeded in breeding this fly.

This species is distinguished from the closely allied *Spathegaster Taschenbergi* and *S. similis* by the ovipositor being longer in proportion, pointed, and straight.

[The April bud-gall is found on *Quercus pubescens* and *Q. sessiliflora*.

Inquilines. *Ceroptres arator* in June of the first year. *Platymesopus tibialis* in May of the first year.]

In the case of those gall-flies which have hitherto been described we have observed this curious circumstance, that they each possess a regular generation-cycle, consisting of two forms more or less distinct.

In one generation only females occur, and reproduction is wholly by parthenogenesis, in the other generation on the contrary both sexes exist, and parthenogenetic reproduction is unknown. This alternation of generations, as it occurs in these species, appeared to me at first to be the natural and universal rule; and I believed that the problem of the position of the so-called agamous gall-flies would be solved by regarding an agamous and a sexual generation as forming a connected generation-cycle. Further observation has however shown me that the existence of alternating generations is not an absolute rule applying to all species of oak gall-flies.

Several agamous species of gall-flies still remain to be described which are not linked to any alternate generation.

These species are few in number, and propagate themselves in an unbroken succession of generations in the female sex. I add the following descriptions of them because it is interesting to compare them closely with the other species. They belong entirely to the genus *Aphilotrix*.

20. Aphilotrix seminationis. Gir.[1]

Gall. Spindle shaped, stalked or sessile, with sharp or scarcely visible longitudinal ridges; green, often tinged with red; at first hairy, especially on the apex, generally smooth later. The gall occurs on leaves as well as on the stems of the flowering catkins. When galls are formed on leaves these undergo striking

[[1] *Cynips seminationis*, Giraud. *Cynips inflorescentiae*, Schltdl. *Andricus seminationis*, Mayr. Cameron considers the fly indistinguishable from *A. quadrilineata*.]

deformities, being sometimes deeply indented or distorted. If the galls are formed on catkin stems, these are often abnormally thickened and remain on the twigs the whole summer, instead of falling off in the usual way as soon as the flowering is over. The galls appear at the end of May, mature in June, and then fall to the ground. (Fig. 20.) This gall has a strong resemblance to the *Aphilotrix callidoma* gall, but is easily distinguished from it by its point of origin; it never grows from a bud like *Aphilotrix callidoma.*

The rearing of the Fly is accomplished without difficulty. The galls when collected should be kept for some time on damp sand, they should then pass the winter in the open air, and in the following April the fly will appear. Some galls remain dormant one whole year, and the fly does not emerge until the second year.

Fly. Size 3-4 mm. long; the colour varies from yellowish brown to dark brown; the lighter specimens have on the mesothorax four black lines of varying breadth, these lines are usually not sharply defined but somewhat blurred; in the darker specimens the lines are scarcely recognizable, the back appearing an almost uniform dark brown, with the scutellum light. The sides of the thorax have white hairs, otherwise it is smooth and shining. Abdomen dark brown above, with the ventral aspect lighter. The legs vary in colour from orange to brown, coxae dark, femora and tibiae black on the outside.

Experimental breeding. I am now enabled to state the mode of propagation of this species with absolute

certainty, a result obtained by experiments in breeding carried on for three consecutive years. The flies emerging in the first half of April soon begin to prick the buds, and this they do in exactly the same way as the genus *Neuroterus*: the ovipositor is pushed under the bud-scales, glides down to the base, and is then bored into the interior of the bud; by this means the egg comes unfailingly to lie on the rudimentary leaf. In 1876 I made my first experiment; from April 3 to 5 several buds were pricked, and on May 28 two *Aphilotrix seminationis* galls were formed. In 1877 seven buds were pricked, between April 13 and 15, from which I obtained in June four *Aphilotrix seminationis* galls. And lastly, in 1878, I made experiments with flies which had been reared from catkin galls, to convince myself of their indentity with those derived from leaf-galls; these flies soon began to prick the buds of an oak sapling, and the result was that in the beginning of June, five *Aphilotrix seminationis* galls were formed on the leaves. There is this peculiarity in the growth of these galls, that after the gall has appeared like a little hairy knob on the unfolding leaf, there is a long pause in its development, and it is quite fourteen days before growth begins again. Those growing on the flower stems have a still longer period of rest, and in these the first sign of gall formation may be simply an enormous thickening of the flower stem.

[The barley-corn gall is found in May on *Quercus sessiliflora* and *Q. pubescens*.

Inquilines. *Synergus albipes* and *S. facialis*, in July of the same year.

Parasite. *Eurytoma rosae*.]

21. Aphilotrix marginalis. Schltdl.[1]

Gall. These conical or oval galls are formed on leaves, often several on one leaf. They are of a green colour, or striped with red; the surface without hairs, but with irregular longitudinal furrows; always sessile and resting on the leaf by a broad base, which indents the leaf surface. They appear in May and mature in June. (Fig. 21.)

Rearing the Fly is carried out in the same way as in the last species; it appears, like it, in April.

Fly. 2·5–3 mm. long; very like the last in colouring. Some specimens are even darker, they can only be distinguished with certainty by the galls. Colour dark brown, the scutellum always pale. The colour of the legs varies from orange to dark brown.

Experimental breeding. I have repeatedly made experiments in breeding this fly. The flies emerging in April soon began to prick the buds, and both in 1876 and 1877 I obtained galls from my experiments. The first sign of gall formation is a little green, or occasionally reddish, thickening of the leaf surface, which quickly grows larger. To enable me more conveniently to compare the formation of this gall with the former, I made a combined experiment, in April 1879, and allowed the last two species to prick the buds of a little oak together. Several buds were pricked under my observation by both flies and

[[1] *Cynips marginalis*, Schltdl. *Andricus marginalis*, Mayr. Cameron considers it *Aphilotrix quadrilineata* occurring on leaves and not a distinct species.]

I allowed them to remain for several days. In May the commencement of gall growth was visible, and the *Aphilotrix marginalis* galls were fully grown by May 30, while the *Aphilotrix seminationis* galls were then only visible as little hairy knobs: the much earlier development of the *Aphilotrix marginalis* gall which enables it to arrive at maturity two or three weeks sooner than that of *Aphilotrix seminationis*, serves as a certain distinction between the two galls.

[The marginal gall is found in May on *Quercus sessiliflora*. Parasite. *Olinx trilineata*.]

22. Aphilotrix quadrilineata. Htg.[1]

Gall. In shape the gall is oval, sometimes almost round; it is smooth or irregularly furrowed and ridged, of a green or reddish colour: it springs usually from the stalk of the flowering catkin, but, exceptionally, from the leaves; it appears in May and matures in June. (Fig. 22.) This gall is so like the last that it cannot be distinguished with certainty from it, and it is possibly identical with it. The *Aphilotrix quadrilineata* gall grows both from the leaves and flowering catkins in the same way as the *Aphilotrix marginalis* and *seminationis* galls. Notwithstanding that this gall is very abundant it is by no means an easy thing to rear the fly. From the majority of the galls parasites are usually obtained; then the larva in a large number of

[[1] *Andricus quadrilineatus*, Hartig. *Cynips quadrilineatus*, Thoms. *Andricus flavicornis*, *A. pedunculi*, *A. ambiguus*, *A. verrucosus*, *A. glabriusculus*, Schenck. The specific name *quadrilineatus* was given to it when it belonged to the genus *Andricus*, and hence it occurs frequently as *Aphilotrix quadrilineatus*, instead of *quadrilineata*.]

instances does not develop into the imago for two years; and should the galls not be kept as nearly as possible in their natural condition they come to nothing. After the galls are collected they must be laid on damp sand until they become brown which is a sign that the larva is full grown; then it is best to put them in a sheltered place in the open air to pass the winter; if these precautions be observed we may reckon with certainty on obtaining the flies in April.

Fly. Size 2–3 mm. long; brownish red; antennae dark; mesothorax marked by four black lines; this sign is very variable, as the two central lines are often merged into each other, although in very pale specimens they are generally plainly distinguishable. Thorax smooth and shining, pleurae somewhat hairy, scutellum rugose; abdomen dark brown above; coxae and base of femora dark, as well as the outer margin of the tibiae; rest of the legs brownish yellow. This species has until now been very variously described; owing to great diversity in the colouring of the fly and in the form of the gall, a large number of varieties have been distinguished, all however belonging to the same species. The most striking thing is that its first describer, Hartig, placed it in the genus *Andricus* because he believed he had found the male. How this error arose I do not know, because it is quite certain that males do not occur, and no entomologist has seen them since. The flies reared from these galls are without exception females.

Experimental breeding with this species is difficult, because the fly is in the habit of pricking the buds

of the male catkins only. The galls are however occasionally found on the leaves, and I thought that I might be successful in getting the fly to produce leaf-galls, but as yet I have only been able to make one experiment, and that gave no result. If it should be proved that *Aphilotrix quadrilineata* can produce its galls as well on leaves as on flowering catkins, this species ought certainly to be united with *Aphilotrix marginalis.* I have repeatedly watched the fly in the open air pricking the flower buds, and I saw it do so on April 13, 1878. The fly is in the habit of concealing itself as much as possible in the daytime, and pricks the buds towards evening. I marked several buds which were pricked before my eyes, and in May I could affirm that *Aphilotrix quadrilineata* galls had been formed, on catkins growing from all these buds.

[The furrowed catkin gall is found in May on *Quercus sessiliflora.*
Inquiline. *Synergus facialis.*
Parasites. *Torymus auratus* and *Olinx trilineata.* The gall is very various in form, as the large number of synonyms indicates.]

23. Aphilotrix albopunctata. Schltdl.[1]

Gall. A very dainty bud-gall, like a miniature acorn; 4–5 mm. long; of a greenish yellow or brownish colour, with pale spots; the apex distinctly umbilicate. The gall appears in the buds in the beginning of May, becomes rapidly mature, and falls to the ground at the end of May. (Fig. 23.)

Rearing the Fly is easy and it emerges in the

[[1] *Cynips majalis,* Giraud. *Cynips albopunctata,* Schltdl. *Andricus albopunctatus,* Mayr. Cameron considers the fly the same as *A quadrilineata.*]

following April, but in this species also a certain number of flies do not emerge until the second year.

Fly. Size 3-4 mm. long; yellowish brown; antennae black except the basal joint which is yellow below; head and thorax yellow; on the metathorax four black lines, either distinct and narrow, or broad, in the latter case the two central ones blending with each other; thorax smooth, hairy at the sides; scutellum rough; abdomen yellow, black above; legs orange; base of the coxae dark. This fly is very like *Aphilotrix callidoma*, but it is distinguished from it by the pale scape of the antennae.

Experimental breeding. I observed this fly for the first time pricking a bud in April, 1875. I made an experiment with several flies in 1876 on an oak sapling, but I obtained no galls although some buds were pricked. In a fresh attempt which I made on April 14, 1877, I placed ten flies on a little oak; they pricked several buds, and I succeeded in getting galls. On May 10, the first gall appeared on a bud, four more followed, and I obtained in all five *Aphilotrix albopunctata* galls, so that there could be no longer any doubt that *Aphilotrix albopunctata* produces the same gall as that from which it emerges.

[The spotted bud gall appears in May on *Quercus pedunculata*, *Q. sessiliflora*, and *Q. pubescens*.

Inquilines. *Synergus facialis*, *S. radiatus*.

Parasite. *Torymus rubricipes*.]

In the preceding pages I have sketched the life-history and manner of propagation of a number of oak

gall-flies, based on observations extending over many years. The species described belong to the fauna of this locality (Schleswig), but at the same time they give a tolerably accurate illustration of the oak gall-flies occurring in the whole of North Germany. I have not as yet been able to make any experiments on the South German species, nor on those occurring only on *Quercus cerris.* There still remains a wide field for observation and discovery.

In order to facilitate reference, I have arranged in a tabular form those species of which the alternate generation is known to exist; and I have placed in a separate table those which are found in one form only.

I. Cynipidae with alternate generations.

No.	Parthenogenetic Generation.	Flies Emerge.	Sexual Generation.	Flies Emerge.
1.	*Neuroterus lenticularis*	April	*Spathegaster baccarum* .	June
2.	" *laeviusculus*	March / April	" *albipes* . .	June
3.	" *numismatis*	April	" *vesicatrix* .	June
4.	" *fumipennis*	May	" *tricolor* . .	July
5.	*Aphilotrix radicis* . .	April / May	*Andricus noduli*	August
6.	" *Sieboldi* . .	April / May	" *testaceipes* . .	August
7.	" *corticis* . .	April / May	" *gemmatus* . .	July / August
8.	" *globuli* . .	April	" *inflator* . . .	June / July
9.	" *collaris* . .	April	" *curvator* . . .	June
10.	" *fecundatrix*	April	" *pilosus*	June
11.	" *callidoma* .	April	" *cirratus* . . .	June
12.	" *Malpighii* .	April	" *nudus*	June
13.	" *autumnalis*	April	" *ramuli*	July
14.	*Dryophanta scutellaris*.	Jan. / Feb.	*Spathegaster Taschenbergi*	May / June
15.	" *longiventris*	Nov.	" *similis* . .	May / June
16.	" *divisa* . .	Oct. / Nov.	" *verrucosus* .	May / June
17.	*Biorhiza aptera* . . .	Dec. / Jan.	*Teras terminalis*	July
18.	" *renum* . . .	Dec. / Jan.	*Trigonaspis crustalis* . .	May / June
19.	*Neuroterus ostreus* . .	Nov. / March	*Spathegaster aprilinus* .	May / June

II. Cynipidae without alternate generations.

No.	Exclusively Parthenogenetic Species.	Emerge.
20.	*Aphilotrix seminationis*	April
21.	,, *marginalis*	April
22.	,, *quadrilineata*	April
23.	,, *albopunctata*,	April
[24.	*Cynips Kollari*	{ Sept. May]

CHAPTER III.

On the Formation of Galls by Gall-Flies.

In the description of the oak gall-flies given in the last chapter, the importance of an accurate examination of the gall is repeatedly enforced. The study of the flies must begin with the galls, they give in all cases the best, and often the only, means of distinguishing closely related species; and lastly they play a most important part in the economy of each species, because they serve as the abode of the individual, as larva and imago, for the greater portion of its life. I will therefore endeavour to give a general idea of the formation of galls.

In spite of great differences in form, manner of formation, size, and appearance, galls can all be referred to a common origin; whether they grow from the bud, leaves, bark, or roots, the parent tissue from which they spring has always the same physiological character. This invariably belongs to that zone of formative cells which is called the cambium-ring; a layer which, beginning from the finest root fibres, and extending to the most distant leaves, wraps the entire plant in a tight-fitting garment. The whole vegetable life proceeds from the cells of the

cambium-ring. These cells are the theatre of actual metabolism; they are not yet differentiated into a stable tissue, but await a period of developmental activity. A tissue that possesses these properties possesses the conditions essential for gall formation. When a gall-fly has inserted its egg into the neighbourhood of this tissue, what follows? In the first place the act of ovipositing of itself has no effect. The wound to the plant-tissue inflicted by a simple prick does not necessarily give the impetus to gall formation. Hitherto it has constantly been stated that the prick of the gall-fly and the simultaneous introduction of a glandular secretion excited a specific cell-growth which led to the formation of the gall. This supposition derived a certain amount of probability from the frequent occurrences in plants of increased cell formation around wounds, as seen in those swellings of the bark that follow a saw cut. Judging by analogous phenomena occurring in animal tissues, it was thought that the cells reacted to the stimulus of traumatic irritation, so that increased metabolism and the production of new cells took place. This was made the foundation of a most misleading hypothesis; it was assumed that gall-flies, by means of a poisonous glandular secretion which they poured into the wound at the time of ovipositing, instituted a specific form of cell activity, and in this way each species produced its own peculiarly formed and equipped gall; hence it was only required to ascribe to each individual species the possession of a specific secretion. This view of gall formation has been supported in recent

times by Lubbock[1], among others; but as early as 1873 Professor Thomas, of Ohrdruff, objected to this explanation of it, and after numerous experiments, I am convinced that the simple prick of the gall-fly does not set up gall formation; this, I hold, only begins when the larva emerges from the egg.

But it is to be observed that in stating this view I limit it to oak gall-flies; there do exist gall-producing flies in another class of hymenoptera, which produce their galls in the way just mentioned. I have carefully observed this in *Nematus Vallisnierii*. This fly, which is armed with a finely serrated terebra, cuts into the tender leaves of the end shoot of the *Salix amygdalina*, and inserts her egg into the open wound, frequently placing several in the same leaf. At the same time some glandular secretion flows into the wounded leaf. A few hours after this injury the leaf surface presents an altered appearance, and new cell formation begins freely, leading to a thickening of the surrounding leaf surface. After the lapse of about fourteen days the green and red bean-shaped gall is fully grown. If it be now opened the egg can still be seen lying within the cavity. The embryonic development is yet unfinished, and three weeks elapse before the larva emerges from the egg, to find around it the material prepared for its nutriment. In this case the wound caused by the fly is the immediate exciting cause of cell activity, and leads to gall formation. In the case of *Cecidomyidae*, belonging to another division of gall-

[1] Sir J. Lubbock. *Origin and Metamorphosis of Insects*, p. 8, 1876.

producing insects, there can be no question of any wound of the plant cells producing the gall, because these minute flies have no piercing apparatus. They are enabled to introduce their egg into an opening bud by means of a long protruded ovipositor, and then it is the emerging larva which first stimulates gall formation. Among gall-flies the same thing takes place, the emerging larva invariably determines gall production, and this can easily be proved. In the course of the experiments in breeding, it was invariably observed that, whether the flies laid their eggs in buds or leaves, the wound was not immediately succeeded by reflex plant growth. If buds in which eggs had been laid were opened, no change was found in the interior of the bud until the larva emerged (except of course the delicate canals pierced by the ovipositor). It is simpler still to observe leaf-pricking gall-flies. If a leaf has been pricked by *Spathegaster baccarum*, the spot where the ovipositor penetrated is quite visible; but during the first fourteen days there is no further change in the leaf surface, and this only begins on the emergence of the larva. Undoubtedly at the time of pricking some secretion from the poison gland reaches the wound, but this merely serves to seal over the cut made by the ovipositor in the leaf surface, and does not stimulate cell activity. This is seen still more strikingly in *Trigonaspis crustalis*. This fly pricks the leaf in May, but months pass before any trace of gall formation can be seen. It has a tolerably strong ovipositor with which it cuts into the veins of the leaf, and in this way a distinct mark is left wherever

an egg has been inserted. Guided by these marks, it is easy to find the eggs, but it is not until September that the larva leaves the egg, and then gall formation begins.

It would naturally be interesting to observe the exact time when the larva quits the egg and starts gall formation; but this is very difficult to do. Whether the egg be enclosed within a bud or a leaf, it is withdrawn from observation, and it is difficult to hit off the exact time when the larva is in the act of bursting the egg. I have several times however been successful in observing this stage in *Neuroterus laeviusculus* and *Biorhiza aptera*. The moment the larva has broken through the egg covering, and has, for the first time, wounded the surrounding cells with its delicate mandibles, a rapid cell-growth begins. This goes on so quickly, that, while the posterior part of the larva is still within the egg-covering, a wall-like growth of cells has already arisen in front. This rapid cell increase can easily be explained, because the irritation set up by the emerging larva is exerted upon highly formative cells, which collectively possess every condition for growth. The cells which are primarily around the larva cannot be distinguished from the parenchymatous cells from which they proceed.

In every gall formation this holds good, and it will be found that the first effect is only an increase of cell formation in the part. A gall is not to be considered as a parasitic growth in the surrounding tissue, but as consisting of the same elements as that tissue, and as substituting itself for them. Therefore the growth of

the gall usually proceeds proportionately to the growth of the cellular layer in which the egg is laid. Let us take the simplest case, that of an egg laid in a leaf. The gall formation begins in the layer of formative cells on the under surface of the leaf, the layers of the upper surface of the leaf are formed of cells which have become stable; they undergo no further change, nor do they respond to any irritation applied to them. They are incapable of forming new cells; any new formation can only originate in the cells of the under surface. At first the gall formation only affects the small zone of cells that surrounds it, but as soon as it acquires a new vascular system of its own it begins to grow apace as an independent structure.

Matters are different when the eggs are laid in the bud, and the emerging larva comes in contact with one of the rudimentary leaves. These consist still of unmodified cells, which are all equally capable of development, whether they occur on the upper or under surface of the leaf; both surfaces consequently take part in gall formation, and when the leaf comes to be unfolded it is found that there is an actual absence of leaf tissue, and that the resulting gall grows through the leaf substance.

It is different again when the egg is laid in the cambium-ring of the bark. Here the cells which first form round the larva cannot be distinguished from the adjacent cells of the cambium tissue, but in the later cell-growth there is a sharp zonal contrast. The peripheral zone of the cambium-ring produces the cells of the bast parenchyma, while the central zone of the

cambium produces the wood parenchyma; and in these galls we have similarly a soft peripheral zone of sappy parenchymatous cells, and a hard central zone of wood parenchyma: and in all bark galls this woody base penetrates more or less deeply into the ligneous tissue of the tree, while the soft fleshy periphery always projects from the bark.

The new cell-growth is arranged in regular concentric layers around the larva, and is accompanied by certain changes in the cell-contents; those cells lying next the larva swell, the cell-contents become cloudy, and exhibit a multitude of starch granules.

The rudimentary gall draws its first nourishment from the surrounding tissues; later it acquires greater independence, for a new element comes to assist in its further development. From the spiral vessels lying in the cambium-ring processes are driven into the rudimentary gall; and the entrance of these vessels always occurs at a definite spot on the lower surface of the gall, whether the connexion with the parent tissue be by a broad base or by a small stalk.

The gall has now become an independent structure, and is practically withdrawn from the direct influence of the cellular area which surrounds it, and from which it sprang.

Its individuality of organization is now displayed by most complicated transmutations of cells originally morphologically alike. This is especially seen in the peripheral cells, which, by assuming peculiar pigments or by developing hairs of various kinds, exhibit an enormous variety of forms. It is still a moot point

in what way that differentiation proceeds which gives to each gall its characteristic form, and regulates its position and season.

It is the value of these different structures, as protective contrivances, which has secured their evolution by the gall.

Pubescence, in particular, assumes an endless variety of forms ; it may appear as a delicate down or as a thick felt: sometimes the hairs exude a sticky sap which deters parasites from approaching the gall ; and even smooth galls like *Aphilotrix Sieboldi* secrete a juice which, as already mentioned, serves to attract ants. These protect them like sentinels, driving other insects off, and often constructing a protective mantle of earth around the galls.

The influence of the larva enters as a necessary factor into the normal course of gall formation. If the larva perishes before the gall is formed, it is well known that a stunting of the gall takes place. It has been already mentioned in the description of *Aphilotrix fecundatrix* that when a roundish, undeveloped, inner gall is found, parasites are always present ; it happens in the same way that when an *Aphilotrix collaris* gall is pricked by parasites, it grows in an anomalous manner, and becomes consolidated with the base of the bud. In the galls of *Aphilotrix Sieboldi* we often find a similar alteration ; for if the gall is pricked by a parasite in the course of its development, it remains small, scarcely projects above the bark, is not regularly striped in the normal manner, and has altogether an appearance so different that it was formerly mistaken for

a new species. At any rate this much is certain, that the influence of the larva is necessary, not only for the early stage of gall formation, but for the completion of its later development. The first cells are arranged in a circle around the larva, and mark it out as the central point which is to dominate their growth in the future.

A circumstance which might lead to serious error ought to be mentioned here. A gall-fly occasionally selects a spot where the formation of an earlier gall has already begun, and on this spot arises its future gall. In one case I was able to observe this satisfactorily. The gall of *Aphilotrix fecundatrix*, which is produced by the little *Andricus pilosus*, is formed at the end of June or beginning of July. At first it is only recognizable by an enlargement or expansion of the bud; but about this time *Andricus curvator* emerges, which also lays its eggs in buds. Owing to the prevalence of the *Aphilotrix fecundatrix* galls it not infrequently happens that *Andricus curvator* lays an egg in the same bud, probably because the ovipositor can penetrate more easily into a swollen bud of this kind. Later we find at the base of the mature *Aphilotrix fecundatrix* gall, and between the bud scales, the *Aphilotrix collaris* gall, which is produced by *Andricus curvator*. I have often found two or three *Aphilotrix collaris* galls in one *Aphilotrix fecundatrix* gall. As the *Aphilotrix collaris* galls are easily overlooked by reason of their minute size, it is obvious that in breeding a doubt might arise as to the origin of the flies. This peculiarity of *Andricus curvator*

making use of the rudimentary *Aphilotrix fecundatrix* galls is also of interest, because it is undoubtedly by a further development of this habit that the inquilines or lodgers have branched off from the *Cynipidae*, to which they are so nearly related. The countless inquilines of the oak gall-flies, which regularly take possession of the great majority of galls, are the worst enemies we have to contend with in our observations. In their whole organization they are so nearly related to the true gall-flies that they can only be distinguished from them by the most minute characteristics, and undoubtedly they have been developed from them. By the use of a gall already formed, the prosperity of their progeny is much more certainly insured; unfortunately, however, inquilines are thus much more easily reared and collected than the true gall-maker.

It is evident from the descriptions of individual galls already given, that they can be produced on all parts of the oak—on leaves, flowers, trunk, root, and buds. In each of these organs the gall-fly finds the same formative zone which only needs the insertion of an egg, and escape from it of a larva, to excite gall formation. We know also that the gall-fly proceeds with judgement in selecting sometimes the tender leaves, sometimes the terminal buds, and sometimes the flower buds for its particular purpose. In spite, however, of every care numerous galls fail, as we have already noted, even where there can be no doubt that the eggs had been laid by the fly.

What causes this frequent failure of the galls? We might at first imagine that there had been some inter-

ference with embryonic development, but I must confess that I have seldom found a dead egg which had not reached development. The cause lies elsewhere. It was constantly remarked that, in the different culture experiments made, the greater proportion of the galls failed. This was most easily observed in the case of flies that produced bud-galls, and which, therefore, lay only one egg in the bud. Naturally the species emerging in summer can only prick winter buds which are awaiting the next period of vegetative activity. In this circumstance we may discover one reason for the failure of the galls, for we may assume that, in many seasons, a premature and anomalous development of winter buds may be absent. But, according to all observations, this cannot be the only reason; indeed, the first essential to insuring gall growth is the right position of the egg. Gall formation will not fail if the larva, when it emerges from the egg, meets with its appropriate cell surroundings; but to secure this the fly must lay its egg with the greatest exactitude. In the case of winter buds, it is especially important that the egg be placed exactly in the zone of the cambium-ring, which lies like a fine seam in the base of the bud. We see that from the winter buds, without exception, only bud-galls, and not leaf-galls, are produced; a proof that the larva has no power to unfold the leaf-germs, but that gall formation can only proceed from the zone of the cambium-ring; and if the egg should not have been laid by the fly exactly where the emerging larva could reach this fine zone, it perishes without forming a gall. If we think of the

great natural difficulties the fly has to overcome in laying the egg with this degree of accuracy, it is not surprising if many eggs come to lie amiss. It is not possible to believe that the emerging larva can alter its position in any way, because it has not the means of locomotion; and, besides, the egg is so closely surrounded by the tissues of the bud that any movement of the larva is rendered impossible.

I certainly believe that failures are most common in those cases where buds are pricked, and where the emerging larva produces a bud-gall; they occur much less frequently in those species which produce leaf-galls, because in these the fly can utilize a much wider territory, extending over the whole of the rudimentary leaves in the bud. But even then it certainly does sometimes occur that eggs are not within reach of the rudimentary leaves, and unavoidably fail. Another confirmation of the view that malposition of the egg is the chief reason for failure of gall formation, is found in the fact that failures are not usually observed in those cases where the fly cannot easily miss the cambium-zone. This is well seen in those species that prick the bark and the surface of the leaf; in these, only the outer layer of epidermis requires to be pierced, and the cell region sought for is always situated about one uniform depth; while in the case of buds of indefinite size and shape, the form of the bud axis, sometimes longer, sometimes shorter, gives a varying measure for the depth to which the egg must be sunk.

The development of the gall is closely dependent upon the vegetative periods of the oak, and ceases with

the close of those periods ; on this account we see that most galls mature in the space of a year. There are some species certainly which require two years, these are always bark-galls ; in the first year the rudiment only of the gall is formed, and its further development is arrested until the next spring, when gall formation is renewed with a fresh period of vegetative activity.

CHAPTER IV.

THE PIERCING APPARATUS.—THE METHOD OF OVIPOSITING.—THE OBJECT AND FUNCTION OF THE EGG-STALK.

GALL formation, as we have seen, is a complicated process, and necessitates the possession of a very elaborate apparatus to ensure the deposition of each egg in exactly the right spot for gall growth. We consequently find that the gall-fly is furnished with a peculiarly constructed piercing apparatus, of which it is necessary that a short description should now be given.

The terebra itself consists of three pieces, for the nomenclature of which we, in Germany, follow Kraepelin[1]; they are a ridged seta[2], and two serrated spiculae[3]. The two spiculae are similar to each other, and the seta is also clearly derived from two symmetrical halves united into one piece. The seta occupies half the area of a tranverse section of the terebra, and the two spiculae together occupy the other half. The terebra is attached to two peculiarly formed chitinous plates which in repose are quite concealed within the

[1] Kraepelin, 'Zeitschrift fur wissenschaftliche Zoologie,' vol. xxiii. Part II. 1872.

[2] Schienenrinne.

[3] Stechborsten.

abdomen. These plates may be distinguished as the anterior (outer) and posterior (inner) plate, a description which is perfectly clear when the ovipositor is placed as it lies in the abdomen of the fly. The accompanying illustrations (Plate III) exhibit the ovipositor always in this position. An examination of the drawings will show that these chitinous plates are found in a great variety of forms, and this variation gives to each species its characteristic formation of ovipositor; but the connexion between them and the terebra is always the same, and the groups of muscles are alike in every ovipositor.

Their connexion with the terebra is as follows—at the origin of each spicula is a broad and almost triangular plate, the angular plate[1] of Kraepelin, which is articulated with the anterior and posterior plates by hinge-joints, but the articulation with the posterior plate is freer and more moveable than with the anterior. This double articulation of the two spiculae has the obvious advantage of enabling them to be thrust to and fro, while they are at the same time securely maintained in position.

There are certain groups of muscles which set the spiculae in motion, but these act primarily through the two plates to which they are articulated. Each muscular contraction causes a movement of the plates which is transmitted to the triangular plate, and thence the motion is communicated to the spiculae by their connexion with the triangular plate. A to and fro movement of the spiculae is thus the only possible one, and at the same

[1] Winkel.

time it is the only movement necessary in the act of ovipositing. Nevertheless, many muscles are required to accomplish this movement.

We pass to the examination of the other portion of the terebra, the seta. The seta is only connected with the two anterior plates, and like the whole ovipositing apparatus, it is throughout composed of two symmetrical halves. From the upper rim of each anterior plate springs what is called the arch, which passes directly into, and is the origin of the seta. The point where the two arches amalgamate is the origin of the seta. On its lower surface, at this point, the seta bears a well marked chitinous projection, called the horn, which is important, because it forms the insertion of a strong muscle. In consequence of its origin and the way in which it is strengthened, the seta possesses only a moderate degree of mobility.

The chitinous framework of the terebra may be seen when it is removed from the body, and it also comes partly into view during ovipositing; but further preparation is necessary in order to see and understand the action of these muscles. To expose them, the two pairs of plates, which are firmly united and enclosed in a chitinous membrane, must be separated in the middle line, when the muscles belonging to each pair of plates will be found placed on their inner surface. In all, we have five pairs of muscles to examine.

Beginning with the anterior plate, we see that the *first muscle*, a very powerful one, takes its origin from the upper third of the plate, and spreading like a many-rayed fan is inserted by a strong tendon into the root

of the seta (called by Kraepelin the horn). By its contraction this muscle draws upon the horn, and thus raises the seta from the position it occupies in repose, and directs it downwards: this is the first introductory movement in ovipositing.

The *second*, a smaller muscle, also takes its origin from the anterior plate, chiefly from the arch, and is inserted by a long chitinous tendon into the base of the horn near the last muscle. The contraction of this muscle draws the seta towards the anterior plate, and it is thus the antagonist of the former one. This muscle also varies greatly in strength, being sometimes reduced to a few fibrillae; in *Neuroterus laeviusculus* it is entirely wanting, and the first muscle is also very feebly developed in this fly.

The *third*, a powerful muscle, arises from the hamular process of the anterior plate and from the margin of the notch in which the angular plate lies; it is inserted, by a long line of attachment, into a strong chitinous ridge on the posterior plate. The contraction of this muscle draws the posterior plate upwards. This movement is communicated to the angular plate, and to the spiculae connected with it, and the result is that these latter are thrust forward. This movement is of the greatest importance, for it is by the spiculae, when thus thrust forward, that the first opening is made, through which the whole ovipositor is pushed into the tissues of the plant.

A *fourth* very powerful muscle springs from the projecting rim of the anterior plate and is inserted into the upper half of the posterior plate. By the contraction

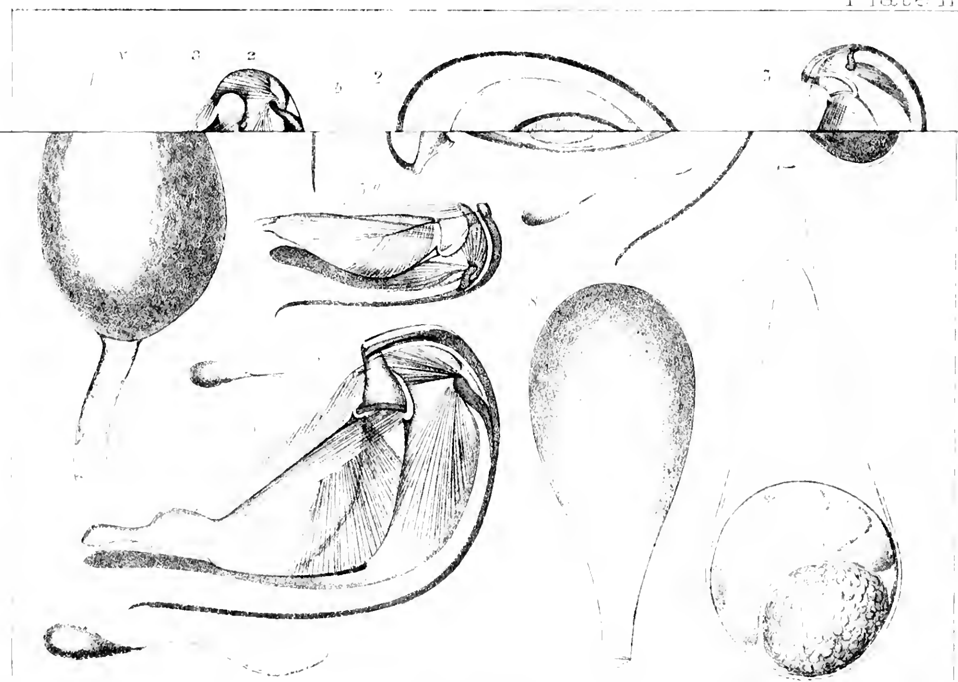
of this muscle, the posterior plate is drawn towards the anterior one, and thus the protruded spiculae are again withdrawn. In this way this muscle is the antagonist of the last one.

A *fifth* muscle springs from the margin of the notch in the anterior plate, near the third muscle, the action of which it supplements.

Owing to their concealed position, it is not possible to observe how these muscles act in the living fly, but the movements of the insect as they occur in egg-laying can nevertheless be seen. They may be watched very plainly in *Neuroterus laeviusculus*. The long ovipositor of this fly (Pl. III, Fig. 2) hidden in the abdomen during repose, comes perfectly into view while ovipositing, and the two pairs of plates are seen at the same time. But as the exact movements of the spiculae are only observable during the slight protrusion of the plates, it is necessary that we should have the plates exposed in order to observe the character of these movements properly. This may be demonstrated in the following way. Wait until the *Neuroterus laeviusculus* pricks the bud, and when the ovipositor has penetrated into the bud, try by a quick movement to pull the fly off; the ovipositor is too firmly fixed, resists, and breaks off[1]. There remains connected with it the whole motor apparatus, and also the large ganglion which innervates the muscles; consequently the pricking movements proceed regularly until the muscles die. It is then

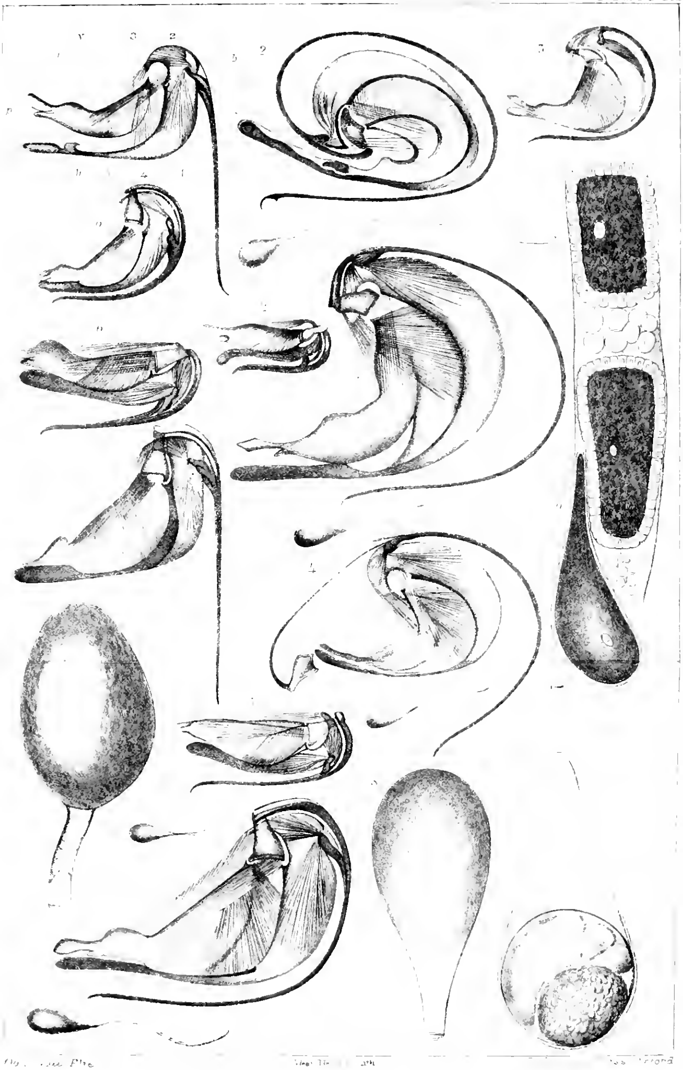
[[1] Lichtenstein states that this often takes place when the flies are at liberty, and in spring he had frequently found the ovipositor and part of the abdomen of a cynips fixed in a bud.]

Plate III



Mintern Bros lith.

Plate III



quite evident that the anterior plate remains always a fixed point, while on the contrary the posterior plate is drawn alternately up and down. By these simple movements of the posterior plate, the insertion and withdrawal of the spiculae are carried on; the thrusting out of the spiculae is the harder operation, and is effected by two powerful muscles; while their withdrawal is easier, and requires only one muscle. The anterior plate remains passive during the act of ovipositing, therefore the seta, which is firmly united to it, takes a less active part; it is pushed steadily forward by the fly and is driven into the canal that has been bored and opened by the spiculae.

We must next inquire into the manner in which the gall-fly introduces the egg into the bud by means of this apparatus. Hartig's explanation, which has hitherto been received, was that the extremely ductile egg was driven through the ovipositor itself. He thought that the contents of the egg passed into the egg-stalk and were collected in its club end, but after the real egg-body had been thrust into the plant tissue, the contents streamed back again into it. Hartig thought this theory all the more probable, because the passage of the yolk into the egg-stalk could actually be observed in the eggs of the Cynipidae. This is easily seen under the microscope if the egg, taken from the ovary, be examined in water. We shall refer later to the meaning of this phenomenon, when we come to compare the length of the egg-stalk with that of the ovipositor, but Hartig's theory must be abandoned as unsatisfactory.

In every case the ovipositor is considerably longer

than the egg, as may be seen by referring to the diagrams in Plate III, where the eggs and ovipositors are all taken from photographs, and are drawn of the same amplification. It follows therefore that one end of the egg cannot be sunk in the plant tissue while the other is still in the canal, and the explanation of Hartig consequently fails.

Besides, it is not possible that the whole egg could be received into the ovipositor and could glide through it, for the ovipositor cannot be compared to a hollow tube. It consists, as already stated, of three parts which are firmly connected with each other. The upper is the ridged seta, on the under surface of which the two spiculae are mortised by two tenons. The seta certainly encloses a central cavity, but it has no connexion with the canal, and merely serves to contain a nerve branch, an air vessel, and some sanguineous fluid. Therefore the egg cannot pass through the ovipositor in the way Hartig supposed. On the other hand, there is sufficient space between the two spiculae to admit the egg-stalk.

It is still difficult to understand how the egg is finally protruded into the bud. We can clearly recognize the movements of the ovipositor made by the fly, but we are unable to follow the movements of the egg, and only in one way do we get any knowledge of this part of the operation. *Neuroterus laeviusculus* requires from fifteen to twenty minutes for the act of ovipositing. If a pricking fly were fixed in position, by being suddenly dipped into chloroform or ether, and the bud were opened, we could then see how far the ovipositor had penetrated, and whereabout the egg was: and if, during the fifteen

or twenty minutes occupied by the laying of the egg, a pricking fly could be fixed in position every successive minute, the buds would yield us a long series of preparations exhibiting the different stages in the birth of an egg. Unfortunately this idea cannot be carried out, on account of practical difficulties. In the first place the time occupied in pricking the buds is not always the same, and in the next each separate act is itself of uncertain duration, since the fly has greater obstacles to overcome in some cases than in others. It is therefore only possible to learn to recognize some of its different stages, and then from these to construct the whole operation.

We shall begin with the moment when the fly places its ovipositor on the bud. She always chooses the edge of one of the outer scales as a point of attack, and pushes her ovipositor under it. Then the ovipositor glides under the scales to the base of the bud-axis. Even this first act requires great strength on the part of the fly. We sometimes see it attack the bud repeatedly with its ovipositor, before it succeeds in getting it under the scales. It does not succeed with buds in which the scales are closely imbricated, hence it always prefers buds with loose-lying scales. When the ovipositor has arrived at the base, it is driven towards the bud-axis so as to reach the rudimentary leaves; but the path made by the ovipositor is always more or less curved. By making a careful preparation of any pricked bud, the canal can be plainly seen, and the path taken by the ovipositor followed. After the fly has finished the first part of its work, and

driven the ovipositor into the centre of the bud, there comes a moment of complete rest, and the fly sits motionless upon the bud. If it is fixed in this position by dipping it into chloroform, nothing is seen of the egg, it still remains in the vagina. Then follows the second part of the work, the pushing of the egg into the bud.

The egg slips, with its enclosed egg-body, to the base of the ovipositor between the origin of the two spiculae. The egg-body glides over the point where the two spiculae embrace the tenon of the seta, since the space remaining open between the two spiculae is too small to admit it. But the egg-stalk, which follows, slips between the two spiculae, is seized by them, and driven forward; in this way the egg is pushed downwards into the ovipositor, with the egg-body hanging out.

When at last the egg is about to enter the canal which has been bored into the centre of the bud, it becomes evident that it is impossible for the canal to admit the ovipositor and the egg-body to pass in at the same time. The egg-body is always of much greater diameter than the ovipositor; on this account the ovipositor is next partially withdrawn by the fly, until the pierced canal becomes empty; the egg-body then enters the pierced canal, and the ovipositor follows, pushing it before it. In short, the whole forward motion is dependent on the egg-stalk being propelled by the to and fro movements of the two spiculae, and the egg reaches the end of the bored canal, while the egg-stalk remains lying within it.

The process of egg-laying, though it seems rather com-

plicated, can be divided into three stages. (1) The canal is bored, the ovipositor gliding under the imbricated scales to the base of the bud, and then being driven into the centre of the bud-axis. (2) The egg passes out of the ovarium to the base of the ovipositor, where the egg-stalk is pinched between the two spiculae, and the egg is pushed along the ovipositor. (3) After the point of the ovipositor is withdrawn, the egg-body enters the pierced canal, and is pushed forward by the ovipositor until it reaches the bottom.

If we consider all this varied procedure, we cannot but be astonished at the accuracy with which the fly carries it out, and repeats it many times in succession. Only one egg can ever pass through the same canal; there is no room for a second, because the egg-stalk of the first egg remains lying in the canal.

Those flies which lay their eggs in leaf surfaces have naturally a much easier task, since they have only to pierce a thin membrane. The mechanism of ovipositing however is exactly the same.

We shall next consider a provision existing in the terebra, by which the fly is enabled to carry out all the operations required in ovipositing, with the greatest exactitude. For this purpose its rigid chitinous armour is furnished with tactile hairs at various points. The tactile organs peculiar to insects consist of fine hairs, connected at their bases with ganglionic swellings of sensory nerve-matter, and they are found at various parts of the ovipositing apparatus. They occur constantly, in all hymenoptera, on the arch of the anterior plate. Their number varies in different species from

twenty to fifty. We must not ascribe any mechanical function in the process of egg-laying to these delicate hairs; they are merely tactile organs, each hair being in connexion with a nerve fibre. These nerve fibres all arise from the large abdominal ganglion, which also gives off motor fibres to the piercing apparatus[1]. The tactile hairs scattered over the arch have the important function of informing the fly as to the true position of the egg. While the egg is gliding over the hard chitinous covering of the ovipositor, the fly only becomes conscious of its progress from one stage to another, when it touches a tactile hair; these serve to signal its advance. Such hairs are consequently placed more closely on the arch, where the egg is caught between the two spiculae; and by their means the fly is guided exactly to where the egg-body is to be found. When the egg has reached the proper point, the egg-stalk is apparently seized by a rapid to and fro movement of the two spiculae. Thus all the time the egg is being pushed down to the ovipositor, there is a provision for keeping the fly informed of its progress by sensation. There are also on the seta, particularly towards its point, organs of sensation, not in the form of hairs but of slight projections of the chitinous membrane. There are besides, in some hymenoptera (*Platygaster*), perfect hairs on the point of the ovipositor. The sensory branches of the nerve, which is contained in the central

[1] In no other order of insects is the abdominal ganglion so powerfully developed as in the hymenoptera; this is due to the fact that it has to undertake the innervation of the complicated piercing apparatus.

canal of the seta, are distributed to these organs of touch. In consequence of this provision, the fly uses the ovipositor as a feeler, and chooses with precision the spot in which the egg is to be deposited. The fly would otherwise fail to find within the bud either the region of the rudimentary leaves, or the meristem in which it is essential that the egg be placed, to secure subsequent gall formation.

A further proof of the delicacy of feeling possessed by gall-flies is shown by the fact, previously mentioned, that many species prick flower-buds only. Here, it is true, the fly also uses its antennae in selecting the buds. If we observe an *Aphilotrix fecundatrix* which has been brought indoors upon a detached bough, we shall see that it is by careful feeling that she finds out the flower-buds, to prick them. Certainly it may happen that she lays an egg occasionally in a leaf-bud, but as if she had found out her mistake, she immediately quits the leaf-bud. During these experiments I tried to find out if it was possible to distinguish between a leaf-bud and a flower-bud, and I discovered that there were certain appreciable differences between them. In flower-buds the mass of rudimentary stamens gives the bud a larger circumference than that of one which contains leaf rudiments. Now in one bud all the leaf rudiments may be supplanted by pollen rudiments, or they may occur together. The greater the proportion of pollen rudiments found in a bud, the more altered is its contour, and the whole bud has quite a different appearance; it is thicker in the middle, and more slender at the apex than other buds. I tried to guess before-hand whether

certain buds were leaf-buds or flower-buds, and in most cases my conjectures were correct. Sometimes even after the fly has closely examined the bud with its antennae, it may happen that the ovipositor, in piercing it, affords different information, and immediately the fly will leave that bud and seek another. The mere fact that several galls occur only on the flowering catkins, shows that the flies know how to distinguish the flower-buds from others.

In the descriptions of oviposition which I have already given, it has been repeatedly shown that it is by means of the egg-stalk being seized by the two spiculae and pushed onwards, that the egg itself is drawn out. But this cannot be the special function and intention of the egg-stalk, as the following facts show. In the first place it is very remarkable that stalked eggs occur only in a small division of the hymenoptera ; and that they are entirely wanting in the *Pimplidae* and *Cryptidae*, which are mostly provided with very long ovipositors. We are justified therefore in concluding that the stalk is not absolutely necessary for the extrusion of the egg.

The eggs of the Cynipidae are further distinguished from the stalked eggs of other hymenoptera in this, that in the former the egg-stalk is attached to the anterior, in the latter to the posterior egg-pole ; consequently at the birth of the egg in the first case, the real egg-body takes the lead ; in the latter, the egg-stalk. This does not agree well with the explanation given by Hartig, who, neglecting the anatomical relations of the parts, assumed that in the Cynipidae also, the egg-stalk was born first. The egg contents according to this ought

to stream first into the egg-stalk and afterwards back into the egg-body. But there is a point of still greater importance—the egg-stalks of Cynipidae are not similar in origin and formation to those of the other hymenoptera. If we examine a stalked egg of *Tryphon*, the stalk is very differently formed; it appears as a solid appendage to the egg-envelope, and is to be regarded as a cuticular formation. It is intended to be bored into the skin of caterpillars. The stalk of Cynipidae eggs has a totally different intention. It is not a simple appendage, but contains a cavity in direct connexion with the yolk sac; and its extremity has a club-like dilatation. Therefore part of the yolk can enter the egg-stalk without difficulty, and, as has already been stated, this actually occurs each time an egg is laid. This peculiar form of egg seen in Cynipidae can easily be recognized within the ovarian follicles in an earlier stage of development. In Plate III, Fig. 9, part of the egg-tube of *Neuroterus fumipennis* is represented exhibiting the origin of the egg-stalk. On the younger egg-germ nothing is yet to be seen of the stalk, and the yolk mass has assumed a cylindrical form; in the more developed egg-cell the flask-shaped form of the yolk shows plainly the egg-stalk in course of formation. Later the younger egg-cells, as seen in the last egg, develop egg-stalks and come to lie finally against the wall of the egg-tube, overlapping each other like tiles. To appreciate exactly the intention of the egg-stalk, it is necessary to observe a still later stage of embryonic development, at which it sometimes occurs that the egg-body expands and enlarges to a remarkable

degree. Compare (Plate III, Fig. 8) the egg of *Biorhiza aptera* taken from the ovary, with another laid in January, and taken out of the bud in the beginning of April. What causes the striking increase in the circumference? Evidently half of the egg is filled with fluid. The embryo lies at the posterior pole, and scarcely occupies half the egg-chamber; in front of it lies a sac containing fluid, which does not enter into the egg-stalk, but stops short at its commencement. The embryo is surrounded by a very delicate membrane, floating, so to speak, in this fluid. The egg-stalk takes part in the expansion, particularly at its club-like end, and is also filled with fluid. What can be the use of this contrivance? We have seen that the club-shaped end of the egg-stalk is the last to enter into the portion of the plant prepared to receive it, and remains close to the surface. It is separated, as a rule, from the outside air by a single thin bud-scale only, and consequently this part of the egg-stalk is accessible to the physical influences of the atmosphere, and admits of gaseous interchange. The fluid in the club-like end, enclosed by a very delicate membrane, can thus absorb oxygen, and as the egg-stalk is merely an extension of the egg cavity, oxygen can be conveyed to the embryo in this way. Therefore, as I understand it, *the egg-stalk has the function of a respiratory organ.*

In support of this theory I would adduce the following facts. The embryo of Cynipidae eggs requires a supply of oxygen at a very early stage of development. A long time before it comes to perfection, it is the seat of continual movements. The *Biorhiza aptera* egg (Pl. III,

Fig. 8) contains an embryo in which the rudiments of the head and mouth are all that can yet be distinguished with certainty; but even at that early period, regular rotation takes place, by which we sometimes obtain a side view, and sometimes a front view of the embryo. These movements follow with a slow, wave-like succession peculiar to sarcode, and are unlike the quick contractions of true muscular tissue. It is possible to observe this embryonic state six weeks before the larva attains perfection. Where such continuous movements are taking place, a supply of oxygen appears to be indispensable. The egg, however, while lying deeply in the heart of the bud, can only obtain this supply of oxygen through the egg-stalk, because no gaseous interchange can take place through the thick walls of the bud. The surrounding plant tissue which is in a state of rest, and in which no metabolism is going on, can afford no such supply. This, it will be seen, imparts a fresh importance to the fact that the egg-stalks are of varying length. If the egg-stalk had only been intended for the purpose of dragging the egg along the ovipositor when it was being laid, a short egg-stalk would have been sufficient. But the lengths are very different, and I believe I can show that they are regulated by the thickness of the layer that separates the egg-bodies from the surrounding atmosphere. As the egg-stalk is a continuation of the yolk sac, and ought to remain in the closest possible relationship with the air, we find that a long stalk is constantly present in eggs which are deeply sunk in the bud. As a rule, a long egg-stalk belongs to a long ovipositor, but there are exceptions, and it is precisely

these which confirm my theory. A glance at the illustration (Pl. III) shows that *Andricus noduli* has a very short egg-stalk with a relatively long ovipositor. We must remember that *Andricus noduli* lays its egg in August, in the cambium layer of the oak bark: but there can be no want of oxygen in a plant tissue in which metabolism is constantly going on, and it is not therefore necessary to inhale oxygen by means of the egg-stalk. The summer generations of many species lay their eggs under the same favourable circumstances as *Andricus noduli*, therefore their egg-stalks are short. But this holds good only of species which lay their eggs in leaves; and we must except those which prick the winter buds. As winter buds are properly speaking resting buds, the surrounding plant tissues can afford no nourishment, consequently the egg-stalk must be long enough to come in contact with the outer air. Against this explanation of the use of the egg-stalk the fact may be advanced that in other hymenoptera this contrivance is wanting, but it would not be difficult to prove that in none of these cases is such an arrangement needed. Thus all the Ichneumonidae give over their eggs to the selected host, and in its body they obtain all the nourishment they require. Many saw-flies also sink their eggs into various parts of the plant, but they do so always at a time when active metabolism is going on. In the case of oak gall-flies on the contrary, the eggs of most of the winter generations are laid at a time when the plants themselves give no signs of life, and when metabolism is dormant.

Another apparent objection is that inquilines closely

allied to the Cynipidae have also stalked eggs. In this case we cannot ascribe to the stalk the important functions of a respiratory organ, as the egg does not need it; but nobody can doubt that their great conformity in outward habit and whole organization proves that these inquilines have been evolved from the Cynipidae, and the peculiarity of the stalked egg has remained with them as a survival. But in their case the egg-stalk is not required to act in the way described, and does not do so; because the peculiar conditions of embryonic development, which we find existing in *Biorhiza aptera*, are wanting in them.

In order to explain the function of the egg-stalk, I have spoken of embryonic development in its advanced stage; but the egg-stalk plays a part also at the moment when the egg is being laid. It has already been explained that the egg cavity communicates with the egg-stalk, consequently part of the contents of the egg can pass without impediment into the stalk. This happens regularly at the laying of each egg. If an egg which has been laid by a fly in a bud, is afterwards removed, the preparation will show the first part of the egg-stalk to be quite full of a finely granular emulsion which forms the egg contents. After a time changes take place in this emulsion, and there are formed in it highly refractive globules of various sizes; finally the whole contents of the egg-stalk clear, and a fine membrane appears, separating the egg-stalk from the egg cavity. These preparatory changes are always a sure sign that egg development is taking its proper course; a matter as to which we may sometimes be in doubt

when we remove a freshly laid egg from a bud, to be further examined in the damp chamber. Although I have frequently observed this occurrence in the egg-stalk, I am unable to explain it more clearly. This much is certain, that it is a phenomenon of great importance, and it is only after it has taken place, that eggs kept in the damp chamber are observed to undergo the various stages of embryonic development. But I have never succeeded, no matter how careful the precautions adopted, or what the modifications under which I carried out the experiment, in bringing an egg to perfect development, after removal from the ovary of a parthenogenetic fly.

CHAPTER V.

Comparative Classification of Corresponding Generations of Cynipidae according to their Organization.

The activity of the fly culminates in the act of oviposition; care for its progeny occupies the whole period of its individual existence. I began therefore by giving a description of the complicated apparatus by which egg-laying was carried out, and I now proceed to compare the whole organization of the two generations in the various stages of imago and larva. I have already described in detail the outward configuration of the gall-flies, and the differences in colouring, sculpture, and pubescence which they exhibit.

Outward characters are usually of little distinctive value in gall-flies; a uniformly dull colour prevails in almost all species; and there are many which cannot be distinguished from each other by an outward examination of the flies only. In comparing two alternating generations, colouring counts for little; their form, structure, and size are of much greater significance. In these respects there are very important differences in the two generations. If a *Neuroterus* and its corresponding *Spathegaster* form be compared with

each other, they could never be mistaken in spite of considerable similarity of colouring. The size may be nearly the same, but the form of the thorax, the cut of the wings, and the configuration of the abdomen are so different, that it would be impossible to confound the two insects. These outward differences are still further confirmed by the form and structure of the ovipositor. The delicate little ovipositor of *Spathegaster* takes up very small space, while the long spirally-coiled ovipositor of *Neuroterus* requires the whole abdominal cavity to contain it, and hence the difference in the contour of the abdomen. Again, the manner in which *Spathegaster* bores into the leaves requires a greater mobility of the abdomen, and so we find it is distinctly pedunculated; *Neuroterus* on the contrary is almost sessile. Lastly, *Spathegaster* selects only leaves of very tender consistence in which to lay its eggs, and must consequently be able to fly easily; we find *Spathegaster* therefore provided with longer and broader wings than *Neuroterus*, which can everywhere find buds in which to lay its eggs, and needs no particular power of flight. While in a manner we can thus construct the whole insect from the ovipositor, it is also possible to distinguish with certainty the various genera by its different methods of action. If two alternating generations live in perfectly distinct outward conditions, it is absolutely essential that the ovipositor should accommodate itself to them, and take that form which is most suitable for the proper insertion of the eggs. If one generation appears at a season when there are only buds to be found, it must be provided with an

ovipositor fitted for piercing buds; and if on the other hand the following generation appears at a season when both buds and leaves are found, a perfectly different form of ovipositor will be necessary for piercing the latter. An accurate knowledge of the ovipositor is of importance in investigating the history of those species of gall-flies whose alternate generation is not yet known. For instance, if a fly is reared from a leaf-gall, and is furnished with an ovipositor which is not adapted for piercing leaves, it may be inferred with certainty that another generation, capable of producing leaf-galls, belongs to this fly.

It will be found of interest, therefore, to review the various forms of ovipositor described.

I. Neuroterus-Spathegaster Group.

A glance at the illustrations[1] of the two ovipositors will enable us to appreciate their great difference. In *Neuroterus laeviusculus* (Fig. 2) the ovipositor is very long and spirally coiled; in *Spathegaster albipes*, on the contrary (Fig. 2[a]), it is short and slightly curved. The other species of *Neuroterus* show a somewhat shorter ovipositor, especially *Neuroterus fumipennis* (Fig. 3). *Spathegaster* ovipositors do not vary. The *Neuroterus* ovipositor has a hook-shaped point, and can therefore never penetrate perpendicularly into a bud. The *Spathegaster* ovipositor, being only slightly curved, can pierce vertically the surface of the leaf.

[1] I may here remark that the illustrations are all drawn from photographs, and therefore give exact relative proportions. The drawings of the eggs near them are also photographed on the same scale.

The different form of the plates in these two ovipositors is especially striking. In *Neuroterus* they are almost circular, and owing to their great curvature, there is no room for the usually strong muscles of the anterior plate (Fig. 1, No. 1). This muscle therefore appears quite rudimentary, and the second muscle which springs from the arch is wholly wanting.

II. The Aphilotrix-Andricus Group.

In this group also, we meet with differences in the ovipositor, but in some cases they are very slight. If we compare the two ovipositors of *Aphilotrix radicis* (Fig. 4), and *Andricus noduli* (Fig. 4^a), a general harmony is observed, but functional differences are easily recognized. The *radicis* ovipositor ends in a sharply curved point, and is consequently not adapted to penetrate perpendicularly into plant tissue; the fly must drive it into the bud in a circuitous fashion. The ovipositor first glides under the bud-scales to the base of the bud-axis, and is then directed upwards. The *noduli* ovipositor, on the contrary, can penetrate perpendicularly into the bark with its straight point. But with ovipositors so much alike as these, it is well to have some further marks of distinction. At the end of the posterior plate, in all gall-flies, there is a little papilla which is distinctly prominent, of slender form, and thickly covered with tactile hairs. The corresponding parts of the ovipositor, and of the two posterior plates, lie closely on each other, but room for the protrusion of the rectum must be left between them. For that reason there is in each plate a little notch,

which is covered by this papilla, and between the two papillae of the posterior plates, we find the aperture of the anus. The shorter the ovipositor, the nearer to the end of the plate is the papilla; the longer the ovipositor, the further up is the papilla situated; we should accordingly expect to find in *Andricus noduli* a relatively long ovipositor. We also know that *Andricus noduli* must bore through the bark, in order to reach the cambium-ring, therefore the ovipositor must be long enough to penetrate a depth of 2 mm. It measures about 2·5 mm., and is thus longer than the whole fly.

In other species of *Andricus*, a relatively short ovipositor is found, and consequently the papilla is placed nearer the end. This can be recognized in the ovipositor of *Andricus cirratus* (Fig. 1). It enables the fly to bore into the winter buds while small and scarcely developed; and in these it is only necessary to penetrate at the furthest 0·5 mm. in order to place the egg in the centre of the bud-axis.

The longer the ovipositor the greater, relatively, will be its spiral curvature; but in order that the passage of the rectum may suffer no infraction, it must always occupy the same position; therefore its aperture is sometimes nearer, and sometimes farther from the ends of the plates of the ovipositor. An examination of the figures in Plate III shows that the length of the plates and of the ovipositors are always the same, because the small processes of the posterior plates form the sheath of the ovipositor, and enclose it when at rest.

However similar in some cases the ovipositors of the two generations may appear, there is a constant

difference; the *Aphilotrix* ovipositor is always curved, and more or less hooked at the point, because, as has been stated, it is never bored directly into the centre of the bud, like the *Andricus* ovipositor, but always in a curved manner.

III. Dryophanta-Spathegaster Group.

In this group the two forms of ovipositor differ markedly from each other, because the method of piercing is quite dissimilar. *Dryophanta* bores into the buds, *Spathegaster* into the veins of the leaf. The former is provided with a very strong ovipositor which is only slightly curved, and particularly straight at the point; the latter with a short one, somewhat hooked at the point. *Dryophanta* behaves differently from those flies, previously described, which pierce buds: it applies its ovipositor perpendicularly to the bud, and bores straight down into it; the egg thus comes to lie in the centre of the bud-axis, or on one of the rudimentary leaves. *Spathegaster* only pierces the epidermis of the leaf-veins, and pushes the egg into the opening it has made.

IV. Biorhiza Group.

In this group we have considered two species, *Biorhiza aptera*, and *Biorhiza renum*, which can scarcely be united in the same genus. This is very evident when we compare the two sexual generations with each other. *Biorhiza aptera* resembles the sexual generation *Teras terminalis* so closely, that any well marked points of

difference can hardly be found; even the ovipositors have the same form. Although the two flies do not pierce the same parts of the plant (*Biorhiza aptera* pricks buds almost entirely, and *Teras terminalis* only the bark), yet the form of the ovipositor is alike, because the parts of the plant they severally attack are pierced perpendicularly. *Biorhiza renum* has a differently formed ovipositor from *Biorhiza aptera*, although it is also intended for piercing buds. On the contrary, *Trigonaspis crustalis*, the sexual generation, has a quite differently shaped ovipositor, which agrees with that of *Spathegaster Taschenbergi*, and like it is destined to pierce leaf-veins. It is evident that variety of form in the ovipositor enables us very easily, in many cases, to separate species which are otherwise very nearly related. Through adaptation to different circumstances, the ovipositor has assumed many modifications of form, while the rest of the fly's organization has remained essentially the same, at least no striking outward deviations are stamped upon it.

It is interesting to compare the two different generations from the standpoint of their accepted systematic classification. So long as classification regarded only outward marks of distinction, heterogeneous species were constantly being put into the same genus. In many classes of insects outward characters alone might amply suffice to separate the species, because their various habits of life, and their different adaptations to them, have served to stamp distinguishing marks upon them; but in those whose habits of life differ less, we cannot expect to find aids to classifica-

tion. Therefore by attending only to outward differences, we may seek out the subtlest distinctions, and yet obtain no certain basis for a true classification. Hitherto, for example, the sexual generations belonging to *Neuroterus* and *Dryophanta* have been united in the genus *Spathegaster*; but one could no more unite two agamous genera, *Neuroterus* and *Dryophanta*, into one genus, than they could the two forms of *Spathegaster*. It certainly cannot be denied that the two *Spathegaster* forms are alike in outward appearance, but the two ovipositors show an important difference: and it is on this character that their separation must be based. It may be objected that a distinction based on the form and structure of the ovipositor is too subtle, but there is no other constant distinguishing mark. The genus *Biorhiza* also contains heterogeneous species. *Biorhiza aptera* and *Biorhiza renum* resemble each other only in outward appearance; their ovipositors are very unlike: and the two sexual generations belonging to them are so different that they could not possibly be united in one genus.

Besides the assistance in differentiation which the ovipositor affords, the manner of gall formation offers an excellent criterion for determining associated species; and with a proper regard to these two features, the classification of the Cynipidae may be successfully accomplished. It must be hailed as a step in advance that analytical tables have been constructed on this basis; Schlechtendal[1], for example, has sketched out a key to the Cynipidae based on their galls.

[1] R. v. Schlechtendal und O. Wünsche, *Die Insekten*, 1879.

One great difficulty in carrying this out is the fact that neither the alternate generations nor the gall formations of all our Cynipidae have yet been discovered. This is especially the case with those species living on *Quercus cerris.* Here therefore there is still open a wide but fruitful field of observation.

The food and manner of living among the Cynipidae present the greatest uniformity, for in all that belongs to the organs of nutrition, only those modifications occur which the actual circumstances of life demand, and hence these organs undergo little variation.

This is especially true of the digestive tract: the parts composing the mouth are all conformable; all the Cynipidae are provided with solid mandibles, in order to cut through the envelope of the gall, which is often very hard. The maxillary and labial palpi alone offer any differences. At first Hartig assigned great importance to the number of joints in the palpi, and employed the variation in the number of these joints as characters. Those given by Hartig have been adopted in the descriptions of later writers, but there is great need for their careful revision. Microscopic preparations of these minute organs are rather difficult to make and have been much neglected. As a rule the two alternate generations have the same number of joints in the palpi. *Neuroterus* and the corresponding *Spathegaster* have each four joints to the maxillary palpi, and two joints to the labial palpi; but the *Spathegaster* corresponding to a *Dryophanta* has, like it, five joints to the maxillary, and three to the labial palpi. There is one exception to this rule, in the generation-cycle formed

by *Biorhiza renum* and *Trigonaspis crustalis*: here the number of joints in the palpi varies; *Biorhiza renum* has four maxillary and two labial joints, while *Trigonaspis crustalis* has five maxillary and three labial.

As regards the joints of the antennae their number is usually the same in the two generations, except again in the case of *Biorhiza renum* and *Trigonaspis crustalis,* when the first has thirteen, and the second fourteen joints in the antennae. There is, moreover, always this difference in the sexual generations, that the male has one joint more in the antennae than the female. From this it will be seen pretty clearly that any characters based on the number of joints, either in the antennae or in the palpi, are not to be relied upon.

The intestinal system of the Cynipidae is simple, uniform in the various species, and very limited in its functions. My own observations agree with those of previous observers, and I can confirm the statement that the Cynipidae, in the perfect state, take no nourishment of any kind, except a little water. The winter generations almost all appear at a time when vegetable life is dormant, and offers no sustenance; but even the summer generations take nothing except water.

Observation shows that all the Cynipidae require water, and imbibe it with pleasure. Unless frequent opportunities of drinking water are afforded, it is absolutely impossible to succeed in experimental breeding. As regards the summer generations, I will not deny that they do occasionally lick the juices which they find on the leaves, but as a rule water is all they want. On being opened the stomach and metenteron

are generally found empty, or containing only a little transparent liquid. By chance there may be found, mingled with this liquid, a little piece of the gall which has been swallowed in gnawing a way out. The whole intestinal tract is short and simple, and the Malpighian vessels are particularly small, few in number, colourless, and transparent. In gall-flies just emerging, we find in the last portion of the intestine the excrementitious products accumulated during the larval period, and these are discharged soon after the flies take wing; the quantity is greater in winter generations which pass through a long larval stage. These excreta are always liquid and transparent, and it may not be out of place here to observe, that there is an arrangement by which regurgitation into the anterior portion of the intestine and stomach is rendered impossible. In the great intestine of insects we find certain ridges, the so-called rectal glands, the use of which, according to Leydig, is enigmatical.

These longitudinal ridges often differ greatly in form and number, but are always found in the same situation, just at the entrance of the great intestine. Leydig expresses a doubt as to their glandular nature, because the essential conditions of a gland are wanting, that is to say, the presence of a secreting epithelium, and the possession of a duct. He considered them rather as respiratory organs, since there are, notably in the larva of the Libellulidae, rectal gills which aid in respiration. The organs were studied and described afresh by Chun[1],

[1] C. Chun, *Rectaldrüsen der Insekten.* Verhandlungen d. Senckenberg. Gesellsch. vol. x. Frankfurt a. M. 1875.

and he came to the conclusion that they were glands possessing a specific active secretion; but it is undeniable that when the intestine of a gall-fly is exposed, immediately after it emerges from the gall, the function of these rectal glands appears totally different. Indeed what we find is, that the termination of the intestine is bulged into a pouch by the liquid excreta; and above that, just where the rectal glands are situated, there is an annular stricture, and consequently a closure of the intestine. These glands therefore possess a mechanism analogous to a sphincter; now since they project into the intestine. and are applied one against the other, whenever the sphincter-like contraction takes place, an obstruction is produced in the intestine, and the excreta cannot regurgitate into the anterior part. Although I have not pursued narrowly the study of these prominences in all the other orders of insects, I am able to state, from the observations I have made, that they are especially well developed in the case of insects which take liquid sustenance, such as Hymenoptera, Diptera or Lepidoptera, and that they appear to be wholly wanting in the Coleoptera. Accordingly I assume that these prominences are only intended to aid in the closure of the intestinal tube; indeed without them it is difficult to see how a re-fouling of the anterior part of the intestinal tube could be avoided, in the case of those insects which accumulate liquid excreta at the lower end of the intestine.

The small amount of nourishment that the Cynipidae take, indicates a brief existence as a perfect insect. Life in both generations is short; that of the winter generation is a little longer than the other, some species

living from two to four weeks. Several of the summer flies are very fragile and do not live many days.

The whole energies of the Cynipidae are devoted to the proper deposition of their eggs. The more easily and quickly the eggs can be laid, the shorter is the life of the individual; this we see exemplified in *Spathegaster*. If on the contrary the act of egg-laying is difficult, and demands much physical exertion, the gall-flies are stronger and live longer; the winter generations, which always have the troublesome task of laying their eggs in buds, have consequently a much more vigorous organization than the corresponding summer generations, and this also enables them to resist the inclemency of a ruder season. A *Biorhiza aptera* fly can prick a bud with the thermometer at freezing point; its summer generation, *Teras terminalis*, would undoubtedly be frozen by the same degree of cold.

Lastly it is important to compare the reproductive organs in the two generations. Here a perfect analogy will be found to exist; the ovaries have the same structure, each contains a corresponding series of ovarian follicles, in which there lie from six to twelve eggs. In a general way the agamous generations have a larger number of eggs than the sexual, and as a rule the number of follicles, as well as the number of the enclosed eggs, is greater.

The muscular vagina, with its glandular appendages, is the same in the two generations. On each side, near the oviduct, a simple glandular tube opens into the vagina. Its secretion probably only serves to furnish a liquid suited to receive the spermatozoa as they escape from

the *receptaculum seminis*, and to help in conveying them to the eggs, which they are intended to fertilize on entering the vagina. Here also it is the rule that these glands are much more developed in the sexual species than in the agamous.

The *receptaculum seminis* is found in both generations. It is interesting to note that it is not absent even in those species which only reproduce themselves parthenogenetically, although in these fertilization never takes place; but on comparison with the *receptaculum* of sexual species, it exhibits a certain amount of atrophy. In the agamous species it appears more or less rudimentary; the sac is collapsed, atrophied, and without pigment, while the glandular appendages are very much reduced in size. But the constant presence of a *receptaculum seminis* shows that, at some antecedent period, males must also have existed.

There are other phenomena still which indicate this. If we observe a fly of an agamous generation, as for example *Aphilotrix radicis*, just as it has emerged from the gall, we see that after a few moments, it extrudes the ovipositor, and remains some time in this position. Why does it do this? The sexual species does precisely the same, and the object of this position is clear; we recognize in it the attitude preparatory to *coitus*, which is only, indeed, possible in this way.

Gall-flies with long ovipositors withdraw the whole of the piercing apparatus into the abdomen in a state of repose; if it were possible for fecundation to take place thus, the penis of the male must necessarily be equal in length to the coiled ovipositor. But it is infinitely

shorter, so that it is only by extruding the ovipositor that the vagina of the female can become accessible to the male. Now, seeing that the agamous generations have retained the habit of extruding the terebra, as an invitation to fecundation, does this not seem to indicate that, at some antecedent period, males must have existed[1]?

We know, besides, that among other Cynipidae, not living on the oak, a solitary male is occasionally found, although reproduction is carried on purely parthenogenetically. I refer to the Cynipidae of the rose, *Rhodites rosae* and *Rhodites eglanteriae*. In both of these there are found solitary males, although it is probable that for a long time *coitus* has ceased to take place.

Lastly, besides those already mentioned there are still two other accessory glands situated in the vagina, a little nearer the origin of the ovipositor, which are easily recognized by their round form and milk-white colour. They contain an abundant secretion closely resembling a fatty emulsion, and this secretion, I am inclined to believe, has the purely mechanical purpose of anointing the piercing apparatus. In the case of certain other Hymenoptera (*aculeata*), we find, at the root of the sting, an oil-gland which lubricates, with its fatty secretion, the spot where the two spiculae are jointed into the grooved seta, and facilitates their to and fro movement. This oil-gland is wanting in the Cynipidae; but it is replaced in them by the pair of glands just mentioned, which are

[[1] According to Lichtenstein this position so modifies the appearance of the insect that Radosskoiosky, a Russian naturalist, has made a new genus 'Manderstjernia' of a cynips having the ovipositor extruded in this way. Bulletin Soc. Imp. des natural. de Moscow, 1866.]

much more developed. For the long and arduous work which they have to accomplish, it is indispensable that the terebra should be well lubricated, so that its functions may be performed with ease and certainty.

The larval state in the two generations presents also some variations; my researches in regard to these are still fragmentary, and I can only note certain isolated points. I will begin with the egg and its evolution.

However variable the duration of development may be after the eggs are laid, as a rule embryonic evolution begins at once, and it has no prolonged period of egg-rest. Even in the case of eggs deposited in the depth of winter, between November and February, embryonic activity goes on from the first. This evolution is naturally slower during the cold season, and conversely in the summer generations it requires much less time, but even among these we have examples of an embryo remaining a very long time in the egg. When we find that an egg laid in December or January requires some months for its embryonic stage, we can understand it, because it is only when plant growth commences, in April or May, that nourishment reaches the embryo. But why should the same thing occur with, for example, the eggs of *Trigonaspis crustalis* laid in the end of May or beginning of June? It seems difficult to explain this long embryonic rest. Three whole months of this latent existence pass away, and it is not until September that the embryo bursts the shell of the egg, and gall formation begins. It is impossible to suppose that the conditions necessary for gall formation are more favourable then than they were some weeks or months

sooner; nay, on the contrary, in September the period of vegetation is on the wane. The most probable explanation seems to be that this peculiarity of embryonic evolution has been inherited from the generation *Biorhiza aptera*, in which the embryonic stage lasts fully four months.

Yet it is necessary to add that this explanation does not hold good for all species; thus, for example, *Dryophanta divisa* has an embryonic stage even more extended, for the eggs are laid in October, and the gall does not develop until May. In the corresponding summer generation (*Spathegaster verrucosus*) the galls are formed at once, and appear four weeks after the eggs are laid.

The eggs of the two generations, which are necessarily always unfertilized in the one, and fertilized in the other, do not present any longer period of rest in the one case than in the other, but on the contrary all show signs of commencing embryonic development immediately after they have been laid. Parthenogenetic eggs, which are almost always laid in the winter, simply exhibit a much slower evolution than fertilized eggs, which are always laid in the summer. Winter eggs thus offer very good subjects for observation, on account of the slow progress of the various steps of development; it is however a tedious and difficult process to extract them from the buds uninjured, and to make good preparations of them. As I have already said, all my attempts to overcome this difficulty, by endeavouring to secure the evolution of eggs taken from the ovary direct, have been fruitless. However simple may appear the circumstances of the

deposition in the bud, I have never yet been able to imitate them artificially. In spite of all the methods employed I have never succeeded, after many days of observation, in seeing even the commencement of yolk segmentation, although in eggs taken from buds I could always reckon with certainty on seeing this take place after twenty hours. I have already explained the important part which the egg-stalk plays at the outset of embryonic evolution.

The larval stage presents differences in the two generations, but they only concern the duration of development, which is very variable. The larvae agree perfectly in their structure and organization; as they all live under similar conditions, no opportunity is offered for any special or varied adaptation to environment. The structure of the mandibles alone differs in some species; thus the larva of *Neuroterus* has strongly toothed mandibles, while that of *Spathegaster* has them simple and unindented. It is the character of the galls that regulates these modifications. When the gall substance is hard, as in the *Neuroterus* galls, the larva is found provided with strong mandibles; if on the contrary the galls are succulent and their walls soft, as in the *Spathegaster* galls, the mandibles of the larva will be found to be simple and less powerful.

The duration of larval evolution varies much in the two generations. In the summer species the larva increases rapidly, and when full grown passes straight into the pupa state. In the winter species the larval stage is infinitely longer, and presents the following varieties:—

(1) The larva developes during the same year and acquires its full growth; then it rests a year, or even more, in the gall (species of genus *Aphilotrix*).

(2) The larva during the first year undergoes only partial development, passes the winter, and does not complete its evolution until the following year.

(3) Larval development undergoes a period of complete suspension after the larva has left the egg and commenced to form the gall. It remains dormant some months, and only begins to grow again when the gall falls to the ground (*Neuroterus*).

The prolonged larva rest of certain species is very curious; and that which is especially remarkable is, that we often see them remain unchanged for three years before they enter the pupa state. Even among species which have no alternate generation, there are some galls from which the fly does not emerge until the third year. From the regularity with which this occurs, it seems to be perfectly clear that there are individual differences in the duration of development, consequently we find that in the same species some individuals will complete their development in one year, while others will require two. The prolongation of the larval stage is a remarkable phenomenon; one would rather have imagined that a short stage would have been of greater advantage to the species, since the gall would have been exposed for a less time to danger from changes of temperature. It is possible for the two generations to complete their evolution in one year, as in the *Neuroterus-Spathegaster* and the *Dryophanta-Spathegaster* groups. It is interesting to find among the genera which have habitually

a two-year cycle, a species in which the greater part of the individuals complete their evolution in one year.

It may perhaps be taken as an indication that at some former time, when conditions of climate were different, a long larval stage was the rule, but that little by little it has diminished, in some already to its full extent, in some only partially, and in others as yet not at all. We must also admit the same view to hold good with regard to the species which have no alternate generation ; with a certain number of individuals the cycle has become annual, with others it is still biennial.

CHAPTER VI.

ALTERNATING GENERATIONS IN OAK GALL-FLIES. THE RELATIONSHIP OF THE PARTHENOGENETIC TO THE SEXUAL GENERATION. HOW IS THIS GENERATION-CYCLE TO BE EXPLAINED?

IT only remains, in conclusion, to review generally the subject of alternation of generations in oak gall-flies, but I would premise that I have chosen the term 'alternating generations'[1] without intending in any way to prejudge the question. It only indicates the possession of cyclical propagation; while the different terms used with regard to this form of propagation, such as alternating generation, heterogenesis, metagenesis, are, although all closely related, each used in a different sense. Lubbock requires, as a necessary condition of alternating generation, that one generation should propagate itself by budding, like Aphides; but with gall-flies propagation by budding does not take place. Although parthenogenesis and budding may not differ in principle, yet there is this important distinction between them, that in the former, embryonic development runs its entire course outside, and in the latter, inside the ovarium. Among gall-flies both generations develop in exactly the same manner. For this reason I cannot agree with

[1] Generationswechsel.

Lichtenstein, who so ably investigated the Phylloxera, in assuming that the agamous generation of gall-flies holds a subordinate position to the sexual generation, in the way that the budding generations of Phylloxera and Aphides do to their winged and sexual generations.

The question of the mutual relationship of the two generations to each other, is of fundamental importance in the inquiry into the origin of alternation of generations. It is necessary therefore next to consider parthenogenesis, in so far as it has a bearing on alternation of generations.

When I first discovered the alternation of generations in gall-flies, I believed in the existence of a definite law, in accordance with which the gall-flies of one generation invariably propagated themselves parthenogenetically, and those of the next generation always sexually. But more extended observation convinced me that there was no such universal law. I soon found that some species continue to propagate themselves by an annual parthenogenesis. This new light led me to investigate more fully parthenogenesis as it exists in other families of Hymenoptera, and I will state briefly the result in so far as of interest to the preceding question.

Parthenogenesis has frequently been observed among saw-flies. Professor v. Siebold showed, by accurate observations made on *Nematus ventricosus*, that parthenogenesis very frequently occurs, although an equal number of males and females exists in this species. I have myself closely investigated another species, *Nematus Vallisnierii*.

In the autumn of 1876, I collected a large quantity of

the well known bean-shaped galls of this species, which are often found very plentifully on *Salix amygdalina*. In May, 1877, I reared the flies, and was able to convince myself that they were all of the female sex. I continued the experiment by putting them on little willow saplings set in pots, and soon observed the flies begin to saw the tender leaves at the end of the shoots, and deposit their eggs in them. At the beginning of July the full-grown larvae from the galls buried themselves in the earth, to assume the pupa state. They remained in this condition for a very short time, and the first flies appeared on July 27. Again they were all females, and began at once to deposit their eggs. By the end of August the galls were fully developed on the leaves which had been pricked, and the larvae betook themselves to the ground in October, to assume the pupa state. In this particular instance, two generations appear yearly, by strictly parthenogenetic propagation; so that while *Nematus ventricosus* only occasionally reproduces itself by parthenogenesis, *Nematus Vallisnierii* habitually does so. At the same time, the occurrence of parthenogenesis in *Nematus ventricosus* shows that it may proceed directly from a sexual generation. Probably this occurs more readily amongst Hymenoptera than amongst any other class of insects, and therefore I should like to add the following observations on *Pteromalus puparum*.

This little parasite lays its eggs in the pupae of different lepidoptera, such as *Vanessa Io, V. polychloros, V. urticae, Pieris rapae*, &c. A single pupa often supplies more than a hundred of these little flies, so that it is not difficult to collect a sufficiency of them.

As a rule the males of this species appear first and may be easily distinguished from the females; it is therefore easy to separate the sexes, and so prevent fecundation. If the unfertilized females are put with the lepidopterous pupae, they usually proceed to pierce them at once. I have frequently tried this experiment, usually with the result that the unfertilized females only produce males. The result of one experiment was as follows.

In the spring of 1876, I collected a quantity of *Pieris brassicae* pupae which had been pierced by *Pteromalus puparum*. At the same time I had reared caterpillars of *Vanessa urticae* which pupated in June. These pupae were pierced by the unfertilized female Pteromali. To be quite sure, I examined the *receptaculum seminis* and was perfectly certain that fecundation had not taken place. These pierced pupae gave the following results.

1st Pupa = 124 ♂.	3rd Pupa = 75 ♂ 5 ♀.
2nd Pupa = 62 ♂.	4th Pupa = 45 ♂ 4 ♀.

I will add an instance from the rose-gall Cynipidae, showing that parthenogenesis is developed directly from the sexual generation. I have experimented with both *Rhodites rosae* and *Rhodites eglanteriae*. I have reared hundreds of the former species, and have received the results of other observers, and they all show that the males occur in a very small proportion, about 2% only. Owing to the rarity of the males, most of the females are unfertilized, a fact which is confirmed by experiment, for all the flies soon after leaving the

galls lay their eggs. The few males that are still produced are thus superfluous, and we can predict that they will probably become extinct in the course of time. In the other species, *Rhodites eglanteriae*, some males have been observed, but after repeated experiments, I have only succeeded in obtaining females.

These facts show that parthenogenesis occurs very frequently among the Hymenoptera, and that it then springs directly from the sexual generation. The result as regards the sex of the offspring is varied, and appears to be subject to no definite law. Among some Hymenoptera, especially among bees, males preponderate when the eggs are unfertilized; among gall-flies females usually preponderate [1]. It appears that where parthenogenesis has been long continued, males ultimately become extinct: they are unknown in *Nematus Vallisnierii*, and in several species of *Aphilotrix*, but it is not utterly impossible that a male might occur. In the alternating generations of gall-flies the case is somewhat different; the agamous generation occurs only in the female sex, while in the sexual generation males and females emerge in equal numbers. Since, however, it is the agamous generation which produces both sexes, we may assume, *a priori*, that in the ovary there are plasms

[[1] Rolph classifies the offspring of parthenogenesis in groups (1) ♂ only; ♀ from fertilized ova (Apidae). (2) One mixed brood (Cynipidae). (3) Mostly ♂, occasional ♀ (Nematus). (4) Most ♀, periodic or exceptional ♂ (Apus). (5) ♀ only (Rotifera).

Ova fertilized by the queen-bee yield workers and queens. If the nuptial flight be prevented, or the queen be old, and her sperm store exhausted, the ova yield drones only; but Blochmann says these ova show two polar bodies. May these be the first polar body divided? If not, is the next generation fertile?]

differentiated into the two sexes, and that these have been inherited from the sexual generation. But with regard to sexual generations which only produce females, we may assume that every egg without exception has been fertilized, and that such eggs, as in the case of bees, invariably produce females.

If we look at these experiments aright, we perceive that parthenogenesis has been evolved in different ways, according to the requirements of each individual case. It is essential therefore to inquire how each species has developed its own mode of reproduction.

I had started on my inquiry into parthenogenesis with the theory that it was on exactly the same level as sexual propagation, and that there could be no criteria by which one generation could be subordinated to the other. But another, and a very important fact, shows that the two generations of gall-flies are co-ordinate the one with the other.

When we try to explain the occurrence, at the present time, of two generations so utterly different from each other as those we find in the oak gall-flies, we are obliged to admit unconditionally, that originally this difference did not exist, but that both generations were similar. For it is a definite law that the offspring inherits, with the greatest constancy, the organization and physical form of its parents. If differences arise between two originally identical generations, we must refer them to an alteration in the external conditions of life. Of these we place first change of climate, for we know from Weismann's experiments on the seasonal dimorphism of certain butterflies, that differences of

climate can give the first impulse towards a separation between the two generations. As for the degree of difference, that is determined by a factor which we cannot make use of with exactness. It is essentially the individual organization of each species, which at one time inclines it to vary, and at another to remain constant. Thus we find that, in spite of the most opposite outward circumstances, almost no difference has taken place in the generation of one species of gall-fly (*aptera—terminalis*); while on the contrary we are struck by the extraordinary differences which have arisen in those of another (*renum—crustalis*).

If therefore the two generations resembled each other to begin with, which I believe cannot be doubted, the inquiry which of the two generations is the original, or which to-day most closely resembles it, becomes of the greatest interest. With regard to this there are two important points to be considered:—

(1) Some species are only propagated parthenogenetically. (In Chapter II four species are described.)

(2) No species of oak gall-fly is known to propagate itself exclusively in a sexual manner. They are only known to do so alternately with an agamous generation in a generation-cycle.

Therefore it seems to me reasonable to infer that the present agamous form is either itself the original form, or if not exactly identical with it, it is at least very nearly related to it.

There are wider questions still which must remain unanswered. It cannot be doubted after all that has been put forward in these pages that parthenogenesis

was a habit which was acquired by degrees, but at what time it became the rule, would be now as difficult to determine, as whether originally there were one or two generations produced in the year. It is probable that at first there was only one generation developed annually, as is still the case with the purely agamous species.

In any case, I consider it certain that parthenogenesis is the primitive mode, and that sexual reproduction is subordinate to it.

It is of the greatest importance to the proper comprehension of the whole subject of alternating generations, to be able definitely to distinguish one generation as the primary one. The important differences existing between the generations of our time undoubtedly demand long periods for their development, while any certain means for estimating such periods are wanting. If gall-flies were found among fossil insects, we should have a definite starting-point, but no such discovery has been made. We only know that in earlier epochs a totally different climate to the present existed; under the powerful influences of a constantly though gradually changing climate this remarkable alternation of generations has been developed, while the adaptation to new conditions of life has left the general organization of the species more or less changed.

A glance at these totally different generations as they now occur shows above all how difficult is the problem to seek

'in der Erscheinungen Flucht den ruhenden Pol.'

By a few traits only, like hieroglyphics sculptured on the stones of antiquity, does alternation of generations demonstrate to us how remote is the period over which the history of its origin extends.

SCHLESWIG,
May, 1880.

POSTSCRIPT.

HOWEVER interesting may be the facts of alternation of generations as they occur in the oak gall-flies, I have no desire to ignore those species which live on other plants, or to omit the study of their evolution.

The rose Cynipidae, of which I have observed three species, *Rhodites rosae*, *eglanteriae*, and *spinosissimae*, are always propagated by one annual generation. It is the same with the species of the genus *Aulax*, *A. rhaeadis* and *A. hieracii*; and with those of the genus *Diastrophus*, *D. rubi* and *D. glechomae*.

On the other hand there is a Cynips on the maple which shows absolutely the same biological cycle as the Cynipidae of the oak. In this species, as in those, one agamous alternates with one sexual generation.

The following is a description of this insect and the history of its development.

1. **Pediaspis aceris**, Förster=*sorbi*, Tischbein[1].

Gall. The gall is found on the roots of the sycamore (*Acer pseudo-platanus*), but it is also met with on the Norway maple (*Acer platanoides*). When solitary, the gall is round, like a pea, and about 5 mm. in diameter. When in clusters, these are found embracing rootlets, even those of 1 cm. in

[1] Dr. Mayr of Vienna, whose works have been of immense service to the study of the Cynipidae, had previously suggested that the two species *Pediaspis* and *Bathyaspis aceris* were two forms of the same insect. His breeding experiments, like my own, have confirmed this hypothesis.

diameter. But they are also found above ground where the root leaves the tree. When they form a cluster around a root, they give rise to a regular cylindrical swelling, which may measure 5 cm. or more in diameter. This gall consists at first of a firm somewhat fleshy tissue, with a small larva chamber, like that of *Biorhiza aptera.* When mature, it exhibits a wrinkled, woody, brown shell, of no great thickness, enclosing a large cavity.

Experimental breeding. The galls mature in Spring, and are best collected in the month of March. They then contain the perfect flies, which have wintered in them. In the month of April they gnaw their way out and quit the gall.

Fly. Length 5 mm.; colour, ferruginous; the face, the parapsidal furrows, a line at the base of the wings, the middle of the sternum, and the metathorax, blackish; the thorax slightly haired above, more strongly so at the sides; scutellum depressed, surface rugose, with a narrow smooth margin; abdomen smooth, slightly shining, the last segments darker above; legs reddish brown, strongly haired; antennae with fifteen joints.

Experimental breeding. It is comparatively easy to rear this fly successfully. My own experiments were made last April. I began on April 12, having prepared for the purpose six small trees of *Acer pseudo-platanus* in pots. The flies placed on the trees began at once busily to examine the buds with their antennae, and prepared to prick them. Their method of setting to work was rather remarkable. When a fly had found a bud that suited her, she placed herself in such a position, head downwards, that she could drive her terebra diagonally from above towards the centre of the bud-axis. She pricked the bud several times, so that a number of eggs were deposited in the same bud.

I could see with the aid of a lens the openings of the little canals pierced by the terebra on the covering of the bud; and an examination of the buds which had been pricked, showed that the eggs had been deposited on the rudimentary leaves. According to this, the galls ought

to develop on the leaf. The first leaves of the pricked trees, which had been kept indoors, unfolded themselves on May 15. I was able to ascertain at once the presence of an abundant formation of galls. One bud alone developed five leaves on which I counted 14, 9, 6, 4, and 2 galls respectively.

On four of the trees there were galls, and on two none. They had however all been pricked alike, but those without galls were almost a month behind the others in growth; I therefore inferred that the larvae, when they escaped from the egg, were unable to find the tissues of the plant in a condition suitable for their development, and consequently perished. The galls thus obtained were those of *Bathyaspis aceris.*

2. Bathyaspis aceris, Förster.

Gall. The gall is formed on the leaves of the sycamore, exactly as the galls of *Spathegaster baccarum* on the leaves of the oak. As the egg is deposited in the centre of the bud, on a leaf as yet undeveloped, the structure of the leaf is always more or less altered by it. As a rule, this alteration is limited, as far as can be seen, to the galls growing through and through the leaf, but sometimes when several galls are situated side by side the leaf is completely crumpled up. It also occasionally happens that the gall is developed on the petiole, which then undergoes an irregular enlargement. The galls which are situated on the leaves are regularly rounded; 5 mm. in diameter; green or greenish yellow, tinted with red on the side exposed to the sun; the surface is very slightly hairy or quite smooth; the walls of the gall when mature are thin, somewhat solid, and enclose the large larva. The fly emerges at the beginning of July.

Fly. Size 2-2·5 mm.; brownish yellow, lighter than the agamous generation. All the body is of the same colour, except the apex of the abdomen, which is a little darker above. Villosity apparent on the face and the sides of the thorax; very feeble or entirely wanting elsewhere. The

M

scutellum depressed, rugose in the centre, surrounded by a well-marked smooth border. Abdomen shining, legs yellow. Antennae with fourteen joints in the female, and fifteen in the male. Colour similar in both sexes.

In this generation the males and females are equal in number, so that fecundation is secured before oviposition.

I have not hitherto been successful in rearing this generation; the fecundated females descend the tree and set about pricking not only the superficial roots but also the base of the tree. I have no doubt that these galls require two years for their development, in the same way as *Biorhiza aptera*.

As *Pediaspis sorbi*, Tischbein, and *Bathyaspis aceris* both belong to the same generation-cycle, there is good reason for abandoning Tischbein's name *sorbi*. There must have been some confusion in the first discovery of this gall, for there is no doubt that it is found only on the sycamore, and not on the mountain ash as was then stated.

A comparison of the two generations shows a sensible divergence in size, in spite of natural characters otherwise sufficiently similar. In the terebrae there is an essential difference, rendered necessary by the nature of the work to be done by each. The organization of the two generations is also quite dissimilar; the agamous lives three or four weeks, while the sexual survives but a few days.

Now if we unite the two generations in the same species, as Dr. Mayr has just done, and with good reason, we ought to remember that we are uniting two forms which are very different. According to the ordinary tests of classification we ought here to make of these two generations what would be considered two 'good species.' And yet this would be a wrong interpretation of facts which at present we must be satisfied to observe. We are still in the stage of observation; and it must be left to some future generation to undertake the explanation of the facts.

SCHLESWIG,
August 1, 1881.

APPENDIX I.

Cynips Kollari[1], Hartig.

Gall. Size 1·5–3 cm. in diameter, spherical, with a well-marked base of attachment at one pole, and a small bifid apex at the other; beneath this is a linear scar, and around it a circle of warty elevations.

The galls may be solitary, or two or more together on the same bud; and each is situated in the axil of a leaf, or several may be found crowded together on a terminal bud, in which case the internodes have been suppressed. The gall contains a central elipsoidal larva chamber, which retains its shape even when the gall itself is compressed and flattened by the growing shoot. The gall appears in June, is golden yellow if grown in the shade, and green if exposed; it matures in September, and becomes brown as the outer layers dry. In this state it may hang on dead branches for three or four years, but the growth of living wood detaches it sooner. If a transverse section of a young gall, 3 mm. in thickness, be made at the end of June, it will be found, according to Beyerinck, to exhibit the following structure: a larva chamber surrounded by (1) a thin layer of primary nutritive tissue, (2) a thin layer of cells containing crystals, (3) a thin layer of primary starch cells, (4) the layers of the cambium ring, (5) a thick layer of large cells rich in tannin and traversed by vascular bundles, (6) a layer of small meristematic cells, (7) colourless hypodermal cells, (8) epidermis with unicellular hairs containing red pigment in their cell contents. In the middle of July the epidermis is thrown off, leaving

[1] Mistaken by Marshall and others for *Cynips lignicola*, Htg., which is not a British species.

the gall of a grass green colour. By August the primary nutritive tissue has disappeared, and secondary nutritive tissue, containing proteids, oil globules, and the so-called brown-bodies, is formed at the expense of the starch. The gall remains soft until almost mature, but at this time, if it be pierced by a needle, a sclerenchymatous layer can be detected covering the nutritive tissue, giving a certain hardness to the larva chamber, and affording a protection against parasites.

The larva chamber is normally single, but occasionally, where the gall-maker has been destroyed, it is found divided radially into several cells inhabited by parasites. The inquilines are usually found in larva chambers arranged around the central chamber, between it and the surface. When twin galls are formed closely together, they occasionally unite and have one larva chamber[1].

Fly. Length 4·8–6 mm. Whole body reddish yellow. Looked at from above, the head appears widened behind the eyes; cheeks half as long as the eyes, without wrinkles; antennae filiform, thirteen-jointed, second joint longer than thick, third joint the longest, twelfth and thirteenth joints partially united. Thorax brown, covered with short hairs, parapsidal furrows complete; scutellum with two thickly haired foveae at its base, metanotum black, vertical, overhung by the scutellum. Abdomen smooth and shining; second segment covering half the dorsum, very dark above, with two large hairy spots; the other segments fringed with silky hairs. Ovipositor long and spiral. Venter exposed. Wings as long as the fly, hyaline, finely haired; radial cellule open at the margin, elongate, with the areolet opposite its base; basal abscissa of the radius angled; cubitus opposite to, but not reaching, the middle of the transverse basal nervure; legs yellow, margin of the fore tibiae fringed with short depressed hairs; hind coxae broad; claws bifid. According to Mayr the fly closely resembles *Cynips corruptrix* Schl.;

[1] Lacaze-Duthers, 'Recherches pour servir à l'histoire des galles,' *Ann. Sc. Nat. Bot.* 1853, p. 291. Beyerinck, M. W., Beobachtungen über die ersten Entwicklungsphasen einiger Cynipidengallen, *Natuurk. Verh. der Koninkl. Akademie*, Deel xxii.

C. aries Gir.; *C. lignicola* Htg.; *C. tinctoria*; *C. caliciformis* and *C. galeata*, Gir.: species only to be distinguished from each other by their galls.

Rearing the fly. The mature galls are collected in September or October, about which time the fly will be found lying with its head towards the equator of the gall in the direction of most easy exit. Where the gall is double, it occasionally happens that a fly gnaws its way into the twin gall. The flies emerge during September and October, live about a month, and prick the buds, laying about 800 eggs. Some flies winter in the galls, and emerge from the end of April to the beginning of June. The large double galls with one larva chamber usually afford only one small gall-maker. If the larvae be removed from the galls in August, after the nutritive tissue of the gall has been consumed, they will be found to complete their development in small pill-boxes, as perfectly as if they had been left in the galls. The parasites and inquilines as a rule emerge in the spring.

Experimental breeding. In 1857 Mr. F. Smith of the British Museum had a bushel and a half of the galls from Devonshire; the flies from these began to emerge in April, and continued to do so till the end of May. He obtained 12,000 examples, all of which were female. He placed sixty galls in separate boxes, and, as soon as the flies came out, he carried the boxes to different localities in the vicinity of London, and placed them on low oak scrub. He revisited the localities in August, and found galls on the same trees in eight cases out of twelve, but no galls on any other trees in their neighbourhood. From these galls he again obtained the same Cynips and once more placed it in isolated situations, with the result that galls were again obtained in the same proportion as before. In no case could there have been, he says, 'any connexion with the male sex, unless that sex be of microscopic dimensions[1].'

In the autumn of 1881, Beyerinck enclosed a number of flies in nets of muslin, strained on wire frames, and these

[1] *Zoologist* 7332, quoted also in *The Entomologist*, vol. vii. p. 251; 1874.

he secured around suitable oak twigs. He never actually succeeded in seeing the egg laid, as the flies are shy in confinement; and in hundreds of buds which he examined he only found the egg in four, and some of these were found the first day the flies were in the nets. The egg is 2·5 mm. long, and can therefore be easily recognized.

On May 28, 1882, the first sign of gall formation was visible. On June 9, the larva was completely walled in, and the larva chamber closed on all sides. In July the tissues above the scar died and dropped off, leaving the bifid apex uncovered, and disclosing a gall 10 mm. in diameter of a grass green colour. In September growth was complete, and in October the gall-fly emerged.

C. Kollari as a rule seeks out a weakly shoot in October, and pierces the petiole of the lowest rudimentary leaflet of a bud, depositing its egg laterally, on the front of the petiole, and between it and the little secondary bud about to form in the axil of this leaflet. A blastem grows up around the egg-body, gradually closing over it, and pressing the larva out of the egg-shell, which is held back by the stalk. As the petiole of the leaf grows, the canal, with the egg-stalk in it, is carried upwards, and the egg-shell is thus torn out of the blastem.

The gall of *C. Kollari* is widely distributed in Italy, France, Austria, Holland, and in Germany as far north as the Elbe. In England it appears to have been introduced at Exmouth about fifty years ago at a time when cloth manufacture was extensively carried on in Exeter, Tiverton, and other towns in the west of England; but whether the gall was first imported for dyeing purposes is not known. Canon Derham does not mention having found it, although he was well acquainted with the Aleppo gall. It spread slowly over the county, and from this circumstance it came to be called the Devonshire gall.

Cynips Kollari created quite as much sensation in its time as the Colorado beetle or the Hessian fly. As late as 1852 it was averred that the gall was utterly destroying the crop of acorns, used for feeding pigs, and that the loss to farmers

would be enormous. Labourers were exhorted to 'rally round the pig.' The destruction of the oak and the ruin of the wooden walls of England were predicted, and it was stated that 'the mischief has increased so alarmingly that unless some effectual stop can be put to the evil, the landowners of Devon, Cornwall, Dorset, Somerset and even Gloucester will have to abandon all hope of raising oak timber[1].' Those who were less easily alarmed pointed out that the galls contained, even when dry, 17 per cent. of tannin, which was a third of that contained in the best Aleppo galls, and as they generally grow within ten feet of the ground, it was only necessary to collect them for ink-making in order to bring about their speedy disappearance. As to the injury to the acorn crop, it was shown that the Cynips prefers young trees or scrub, while an oak seldom produces acorns until it is fifty years old; so that although few acorns were found on galled trees, those were trees on which no acorns were to be expected.

The gall has now spread steadily over the whole of England and Scotland. In hard winters titmice and squirrels destroy large numbers of them, cracking them up and picking out the larvae.

Inquilines. *Synergus Reinhardi*, *S. melanopus* in May and June of second year. *S. pallicornis* from April to June of second year. *S. facialis* and *Ceroptres arator*.

Parasites. *Torymus regius* (*Devoniensis*), *Megastigmus stigmaticans*, *Decatoma* ?sp., *Macrocentrus marginator*.

Mr. Fitch[2] gives the following parasites: *Ormyrus punctiger*, 18 June—29 July; *Eurytoma* ?sp., 18 April; *Pteromalus tibialis*, *Callimome* ?sp., 28 April—20 June; *Callimome* ?sp., 3-17 April; *Entedon* ?sp., *Eurytoma rosae*, *Syntomaspis caudata*, *Homalus auratus*, *H. coeruleus*, *Odynerus trifascatus* and the bee *Prosopis rupestris*.

Many insects pupate in the empty galls; these include, besides hymenoptera, numerous lepidoptera and beetles.

[1] Mr. Rich at Entomol. Soc., London, Nov. 6, 1854. *Entomol.* vol. vi, pp. 275-338; vii, p. 245; *Gardener's Chronicle*, 1854, p. 742; 1855, p. 789; 1860, p. 72; 1862, p. 813.

[2] *Entomol.* 1879, p. 113.

APPENDIX II.

SYNOPTICAL TABLE OF OAK GALLS.

I. ON THE LEAF.

A. **On the under surface of the leaf.**

(*a*) Currant-like, green often tinged with crimson, less than 6 mm. in diameter, in May and June.
Smooth and glabrous, 5-6 mm.
1[a]. *Spathegaster baccarum.*

Pale, 4 mm., covered with erect white hairs falling off at maturity. 4[a]. *Spathegaster tricolor.*

(*b*) Cherry-like, 1-2 cm., July—Oct.
14. *Dryophanta scutellaris.*

5-7 mm., red with white stripes, skin rough and nodular. 15. *Dryophanta longiventris.*

(*c*) Like buckshot, broader than high, smooth, shining, red becoming brown, July—October.
16. *Dryophanta divisa.*

(*d*) Ovoid, smooth, greenish, then brown with red spots, on vein, between two brown scales, Aug. and Sept., 2-3 mm. 19. *Neuroterus ostreus.*

(*e*) Kidney-shaped, 1-2 mm., green, crowded on veins, in September and October. 18. *Biorhiza renum.*

(*f*) Flat, circular, lenticular, often irregular.
Sunk in the leaf-substance, green, radiate striation, May and June. 3[a]. *Spathegaster vesicatrix.*

Not sunk, attached by a point, covered with golden silky hair, round, centre depressed, in Autumn. 3. *Neuroterus numismatis.*

Not covered with golden silky hair, flat, almost glabrous, margins turned up, centre bossed. 2. *Neuroterus laeviusculus.*

Covered with stellate hairs, top convex. 1. *Neuroterus lenticularis.*

Top concave, bottom pilose, edges curled up. 4. *Neuroterus fumipennis.*

B. **On margin of the leaf.**

No inner gall :

ovoid, smooth, 1–2 mm., June and July, *N. albipes.*

spindle-shaped

shortly-stalked, green with red ribs, apex pointed, 6–8 mm., May—June. 20. *Aphilotrix seminationis.*

not stalked, oval, granular, glossy, green or reddish, spotted, brown when old, 4 mm., May, on half-grown leaves, shoots or buds. 16ª. *Spathegaster verrucosus.*

glabrous, green striped with red, longitudinally ribbed, 4–5 mm., May and June, on fully developed leaves, always sessile. 21. *Aphilotrix marginalis.*

With an inner gall :

Irregular, round or oval swelling at base of leaf, green with large cavity containing small brown inner gall in May. 9ª. *Andricus curvator.*

C. **In the midrib or leaf-stalk.**

Small elongated tumid thickening of mid-rib or leaf-stalk. 6ª. *Andricus testaceipes.*

II. On Buds.

Polythalamous : large spongy, apple-like, on terminal buds in May. 17ª. *Teras terminalis.*

Monothalamous : in May, waxy, not spongy, on twigs on trunk or near ground, 5–7 mm.
18[a]. *Trigonaspis crustalis.*

Pilose and ovate.

Violet with short velvety pubescence in May or June, 2–3 mm. 14[a]. *Spathegaster Taschenbergi.*

Greenish, 2 mm. May and June.
15[a]. *Spathegaster similis.*

Like marbles, on twigs, dark green or brown, 1·5–3 cm., June—September. 24. *Cynips Kollari.*

Small ovate or elongate, dropping when mature :

Glabrous—

Spindle-shaped, longish peduncle, 7–12 mm., green with red ribs, July and August.
11. *Aphilotrix callidoma.*

Peduncle short, September and October, 6-8 mm.
12. *Aphilotrix Malpighii.*

Gall not enveloped in leaf-scales :

Small, granular, 1–2 mm., green then brown, June—August. 7[a]. *Andricus gemmatus.*

Obovoid, green with white spots, pointed apex, 5-6 mm., May and June.
23. *Aphilotrix albopunctata.*

Gall wholly enveloped in leaf-scales :

Hop-like 20 mm. 10. *Aphilotrix fecundatrix.*

Gall partially enveloped in leaf-scales :

Gall pea-like, green, thin-walled, April or May.
19[a]. *Spathegaster aprilinus.*

Globular, tapering to apex, hard and woody, September, 3–4 mm., green, smooth when young, and reticulated when old, apex only appearing beyond bud, blunt. 8. *Aphilotrix globuli.*

Ovoid apex pointed and darker than rest of gall, Sept. 9. *Aphilotrix collaris.*

Apex not ending in dark point, October.
13. *Aphilotrix autumnalis.*

Apex of a terminal twig inflated, longer than broad, large cavity with loose, small inner gall, June.
8a. *Andricus inflator.*

Irregular swellings on twig, petiole, or mid-rib, June.
5a. *Andricus noduli.*

III. ON ROOTS.

Polythalamous, woody when mature, large, brown, irregular, 1-3 inches, on roots, Oct.
5. *Aphilotrix radicis.*

Monothalamous: on rootlets, often in clusters, irregular, Sept. 17. *Biorhiza aptera.*

IV. ON BARK AND THICK ROOTS.

Or on scars, egg-shaped, becoming honey-combed when old. Sept. 7. *Aphilotrix corticis.*

On young branches, like barnacles, red when young, brownish when old, often covered with gummy secretion, June—Aug. 6. *Aphilotrix Sieboldi.*

V. ON CATKINS.

In a mass of woolly hair.

Mass agglomerated, dense, 20 mm., June.
13a. *Andricus ramuli.*

Hair scanty, May and June.
11a. *Andricus cirratus.*

Not in a mass of woolly hair.

Pilose, brownish, 2 mm., oval, May and June.
10a. *Andricus pilosus.*

Glabrous:

Currant-like, May. 1a. *Spathegaster baccarum.*

Spindle-shaped, short peduncle, green with red ribs, apex pointed, 6-8 mm., May and June.
20. *Aphilotrix seminationis.*

Obovoid, ribbed sides, base not contracted, 3 mm., May. 22. *Aphilotrix quadrilineata.*

Sides not ribbed, 1-2 mm., in May.
12a. *Andricus nudus.*

APPENDIX III.

CLASSIFICATION OF THE CYNIPIDAE [1],

WITH THEIR FOOD PLANTS [2].

GENUS.

1. ESCHATOCERUS, Mayr.
   E. acaciae, Mayr (Acacia), South America.

2. PEDIASPIS, Tischbein = BATHYASPIS, Förster.
   P. sorbi, Tischb., agamous form of the sexual
   B. aceris, Först. (Acer pseudo-platanus), Europe.

Species with alternate generations.

3. BELENOCNEMA, Mayr.
   B. Treatae, Mayr (Quercus virens), N. America.

[1] In the case of species with alternate generations the two names under which they were formerly known are retained. The genera and species are described in Prof. Mayr's monographs and in Cameron's *Phytophagous Hymenoptera*, Ray Society.

[2] Where the food plant is *Quercus robur*, so far as the facts have been recorded, the particular trees on which the galls grow have been mentioned in the notes, but it is not to be understood that they are never found on other varieties. The most common variety in England is *Quercus pedunculata*; it is recognized by the leaves being sessile or nearly so, their upper surface being slightly polished, and by the acorns having long peduncles. In *Q. sessiliflora* the acorns are sessile; while the leaves are on long stalks and have their upper surfaces highly polished. *Q. pubescens* is like the latter variety, but has a smaller leaf with a woolly under surface. Oaks usually begin to flower when about thirty years old, but flowers are occasionally found in a very dry season on much younger trees.

GENUS.

4. RHODITES, Hartig.

bicolor, Osten-Sacken	(Rosa)	N. America.
centifolia, Hartig	(„)	Europe.
dichloceros, O.-S.	(„)	N. America.
eglanteriae, Hart.	(„)	Europe.
Mayri, Schlecht.	(„)	„
rosae, Lin.	(„)	„
rosarum, Giraud	(„)	„
spinosissimae, Giraud	(„)	„
verna, O.-S.	(„)	N. America.
ignota, O.-S.	(„)	„

5. TIMASPIS, Mayr.
   - *lampsanae*, Kursch (Lapsana communis).
   - *Phoenixopodos*, Mayr (Phoenixopus vimineus), France (sea-shore).

6. PHANACIS, Förster.
   - *centaureae*, Först. (Centaurea scabiosa), Europe.

7. AULAX, Hartig.
   - *areolatus*, Giraud.
   - *glechomae*, Lin., Hart. (Glechoma hederacea).
   - *graminis*, Cameron (Triticum repens).
   - *hieracii*, Lin., Bouché = *Sabaudi*, Hart. (Linaria vulgaris, Hieracium murorum, H. umbellatum).
   - *hypochoeridis*, Kieffer (Hypochoeris radicata).
   - *jaceae*, Schenck = *affinis*, Schenck (Centaurea jacea).
   - *Kerneri*, Wachtl (Nepeta pannonica).
   - *Lichtensteinii*, Mayr (Centaurea salmantica).
   - *minor*, Hart. (Papaver rhoeas).
   - *papaveris*, Perris (Papaver dubium).
   - *rhoeadis*, Hart. (Papaver rhoeas).
   - *Rogenhoferi*, Wachtl (Centaurea scabiosa).
   - *salviae*, Gir. (Salvia officinalis).
   - *scabiosae*, Gir. (Centaurea scabiosa).
   - *scorzonerae*, Gir. (Scorzonera humilis).
   - *serratulae*, Mayr (Serratula heterophylla).
   - *tragopoginis*, Thoms. (Tragopogon major).
   - *valerianellae*, Thoms. (Valerianella olitoria).

GENUS.

8. Xestophanes, Först.
   potentillae, Vill. = *abbreviatus*, Thoms. ? (Potentilla reptans).
   brevitarsis, Thoms. = *Tormentillae*, Schlecht.
   foveicollis, Thoms. (Potentilla reptans).

9. Periclistus, Först. Inquilines of Rhodites galls.
   Brandtii, Ratz.
   caninae, Hart.
   sylvestris, O.-S. N. America.
   pirata, O.-S.

10. Rhoophilus, Mayr.
    Loewi, Mayr (Rhus lucidum), Africa.

11. Ceroptres, Hartig (Inquilines, lodger parasites).
    arator, Hart.
    cerri, Mayr.
    clavicornis, Hart.
    melanocerus, Hart.
    socialis, Hart.

12. Synergus, Hartig (Inquilines).
    albipes, Hart. = *erythrocerus*, Hart.
    apicalis, Hart. = *immarginatus*, Hart. = *erythrostomus*, Hart.
    evanescens, Mayr.
    facialis, Hart. = *bispinus*, Hart. = *Diplolepis gallae pomiformis*, Boyer de Fonscolombe.
    flavipes, Hart.
    Hayneanus, Hart. = *rugulosus*, Hart.
    incrassatus, Hart.
    lignicola, O.-S. N. America.
    melanopus, Hart. = *Diplolepis rufipes*, Boyer = *Synergus orientalis*, Hart. = *S. socialis*, Hart.
    nervosus, Hart. = *S. tibialis*, Hart. = *S. nigricornis*, Hart.
    pallicornis, Hart. = *S. australis*, Hart. = *S. nigripes*, Hart.

GENUS.

12. Synergus (*continued*).

pallidipennis, Mayr.
physoceras, Hart.
radiatus, Mayr.
Reinhardi, Mayr.
rotundiventris, Mayr.
ruficornis, Hart.
Thaumacera, Dalman = *S. Klugi*, Hart. = *S. luteus* Hart. = *S. carinatus*, Hart.
tristis, Mayr.
Tscheki, Mayr.
variabilis, Mayr = *Diplolepis gallae pomiformis*, Boyer.
varius, Hart.
vulgaris, Hart.

13. Sapholytus, Först. (Inquilines).

connatus, Hart. = *S. erythroneurus*, Hart.
Haimi, Mayr.
undulatus, Mayr.

14. Synophrus, Hartig.

politus, Hart.

15. Diastrophus, Hartig.

cuscutaeformis, O.-S. America.
Mayri, Reinhard (Potentilla argentea), Europe.
nebulosus, O.-S. America.
potentillae, Bassett. America.
radicum, Bassett. America. (Rubus villosus.)
rubi, Hart. (Rubus caesius, fruticosus, and Pteris aquilina), Europe.
turgidus (Rubus strigosus).

16. Amphibolips, Reinhard.

ilicifolia, Bassett. America. (Quercus ilicifolia.)
inanis, O.-S., Bassett. America.
prunus, Walsh. America.
sculpta, Bassett (Q. rubra et ilicifolia).
spongifica, O.-S., sexual form of *C. aciculata*, O.-S. (Q. tinctoria).

GENUS.
17. ANDRICUS, Hart. = CALLIRHYTIS, Först. = APHILOTRIX, Först.

Species with alternate generations.

AGAMOUS.			SEXUAL.
Aphilotrix			*Andricus*
A. autumnalis, Lin.,	alternates	with	*A. ramuli.*
A. callidoma, {Adler (not Gir.)}	„	„	*A. cirratus.*
A. collaris, Hart.	„	„	*A. curvator.*
A. corticis, Lin.	„	„	*A. gemmatus.*
A. fecundatrix, Hart.	„	„	*A. pilosus.*
A. globuli, Hart.	„	„	*A. inflator.*
A. Malpighii, Adler	„	„	*A. nudus.*
A. radicis, Fal.	„	„	*A. noduli.*
A. Sieboldi, Hart.	„	„	*A. testaceipes.*

Species of which the alternate generations are yet unknown.

AGAMOUS.

albopunctatus, Schlecht.
callidoma, Giraud (not Adler).
clementinae, Giraud.
glandulae, Hartig.
kirschbergi, Wachtl.
lucidus, Hart.
marginalis, Schlecht.
Mayri, Wachtl.
quadrilineatus, Hartig.
rhizomae, Hart.
Seckendorffii, Wachtl.
seminationis, Adler.
serotinus, Giraud.
solitarius, Fonscol.
urnaeformis, Mayr.

SEXUAL.

Adleri, Mayr.
aestivalis, Giraud.
amenti, Gir.
burgundus, Gir.

GENUS.

17. ANDRICUS (*continued*).

circulans, Mayr.
crispator, Tschek.
cryptobius, Wachtl.
cydoniae, Gir.
grossulariae, Gir.
multiplicatus, Gir.
occultus, Tschek.
Shröckingerii, Wachtl.
singulus, Mayr=*singularis*, Mayr.

American Species.

acinosus, Bassett.
californicus, Bassett.
capsula, Bassett.
concinnus, Bassett.
flocci, Walsh.
forticornis, Walsh.
ignotus, Bassett.
Osten-Sackenii, Bassett (Q. ilicifolia et coccinea).
petiolicola, Bassett (Q. bicolor).
singularis, Bassett (Q. rubra).
tubicola, O.-S.

SUB-GENUS CALLIRHYTIS.

European Species.

glandium, Gir.
Hartigi, Först.

American Species.

agrifoliae, Bassett.
clavula, Bassett (Q. alba).
cornigera, O.-S. (Q. palustris).
futilis, O.-S. (Q. alba).
operator, O.-S., sexual of *C. operatola*, Riley, Q. ilicifolia.
punctata, Bassett.
quercus palustris, O.-S. ?
scitula, Bassett (Q. coccinea, rubra et tinctoria).

GENUS.

17. ANDRICUS (*continued*).
seminator, Harris (Q. alba).
similis, Bassett (Q. ilicifolia).
spongifica, O.-S. (Q. tinctoria).
Suttoni, Bassett.
tumifica, O.-S.

18. CYNIPS, Lin., Hartig.
aciculata, O.-S., agamous form of *A. spongifica*, O.-S.
amblycera. Gir.
argentea, Hart. = *Rosenhaueri*, Hart.
aries, Gir.
caliciformis, Gir.
calicis, Burgsd.
caput-medusae, Hart.
conglomerata, Gir.
conifica, Hart.
coriaria, Hart.
corruptrix, Schlecht.
galeata, Gir.
glutinosa, Gir.
Hartigii, Kollar.
Hungarica, Hart.
inanis, O.-S. (Q. rubra).
Kollari, Hart. = *Hispanica*, Hart.
lignicola, Hart.
operatola, Riley, agamous form of *A. operator*, O.-S
polycera, Gir.
prunus, Walsh.
strobilana, O.-S.
tinctoria, Lin.

19. APHELONYX, Mayr.
cerricola, Gir.

20. ACRASPIS, Mayr.
erinacei, Walsh.
pezomachoïdes, O.-S.

GENUS.

21. TRIGONASPIS, Hartig = BIORHIZA, Westw. partim.

Species with alternate generations.

crustalis, Hart., alternates with the agamous *B. renum*,
synaspis, Hart.

22. BIORHIZA, Westw. = APOPHYLLUS et TERAS, Hart. = DRYOTERAS, Förster.

Species with alternate generations.

aptera, F., alternates with sexual *Teras terminalis* (Quercus, Fagus, Pinus, and Vitis),
forticornis, Walsh, American.

23. CHILASPIS, Mayr.
nitida, Giraud.

24. PLAGIOTROCHUS, Mayr.
cocciferae, Licht.
ilicis, Licht.

25. LOXAULUS, Mayr.
mammula, Bassett. N. America.

26. DRYOCOSMUS, Giraud = ENTROPHA, Förster.
cerriphilus, Gir.
nervosus, Gir.

27. HOLCASPIS, Mayr.
duricoria, Bassett. N. America. Q. bicolor.
globulus, Fitch.
rugosa, Bassett.

28. DRYOPHANTA, Förster = LIODORA, Först.

Species with alternate generations.

AGAMOUS.		SEXUAL.
D. divisa, Hart.	alternates with the sexual	*Sp. verrucosa.*
scutellaris, Hart.	„ „	*Sp. Taschenbergi.*
longiventris, Hart.	„ „	*Sp. similis.*

GENUS.

28. DRYOPHANTA (*continued*).

Species of which the corresponding generations are yet unknown.

European.

D. agama Hart.
cornifex, Hart.
cylindrica, Licht. on Q. coccifera.
dysticha, Hart.
flosculi, Gir.
pubescentis, Mayr.

American.

D. bella, Bassett.
gemmula, Bassett.
nubila, Bassett.

29. NEUROTERUS, Hart. = SPATHEGASTER, Hart. = AMERISTUS, Först. = MANDERSTJERNIA, Radoszkowsky.

Species with alternate generations.

AGAMOUS.		SEXUAL.
N. fumipennis, Hart.	corresponding to	*Sp. tricolor*, Hart.
N. laeviusculus, Schenck	,, ,,	*Sp. albipes*, Schenck.
N. lenticularis, Oliv.	,, ,,	*Sp. baccarum*, Lin.
N. numismatis, Oliv.	,, ,,	*Sp. vesicatrix*, Schlecht.
N. ostreus, Htg.	,, ,,	*Sp. aprilinus*, Gir.

Species of which the corresponding generations are not yet known.

European.

AGAMOUS.

lanuginosus, Gir.
macropterus, Hart.
saltans, Gir.

SEXUAL.

aggregatus, Wachtl.
glandiformis, Gir.
obtectus, Wachtl.
Schlechtendali, Mayr.

GENUS.

29. NEUROTERUS (*continued*).

American.

balata, Fitch (Q. alba).
floccosus, Bassett.
majalis, Bassett (Q. alba).
minutus, Bassett (Q. alba).
noxiosus, Bassett.
Rileyi, Bassett.
vesicula, Bassett.

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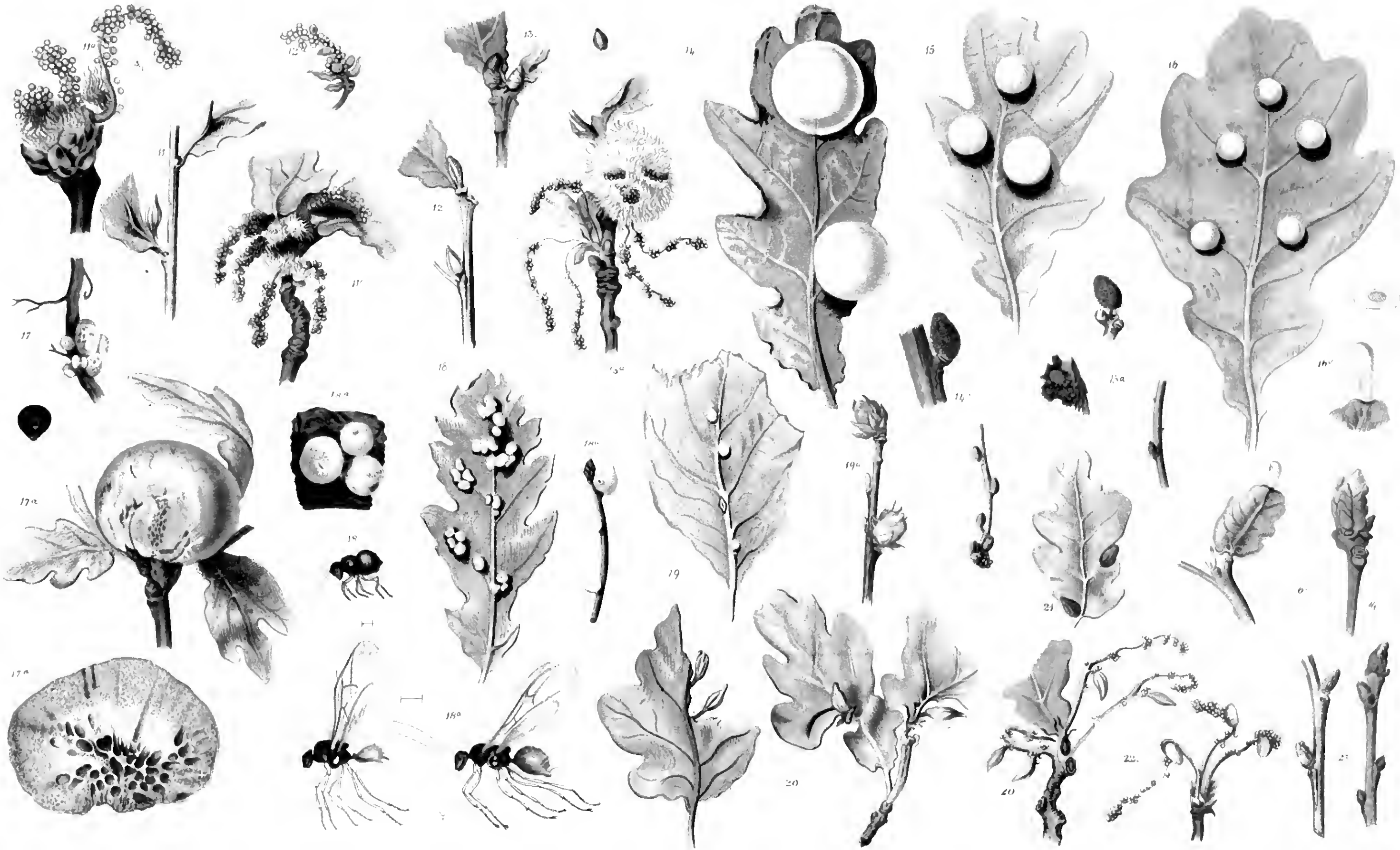

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